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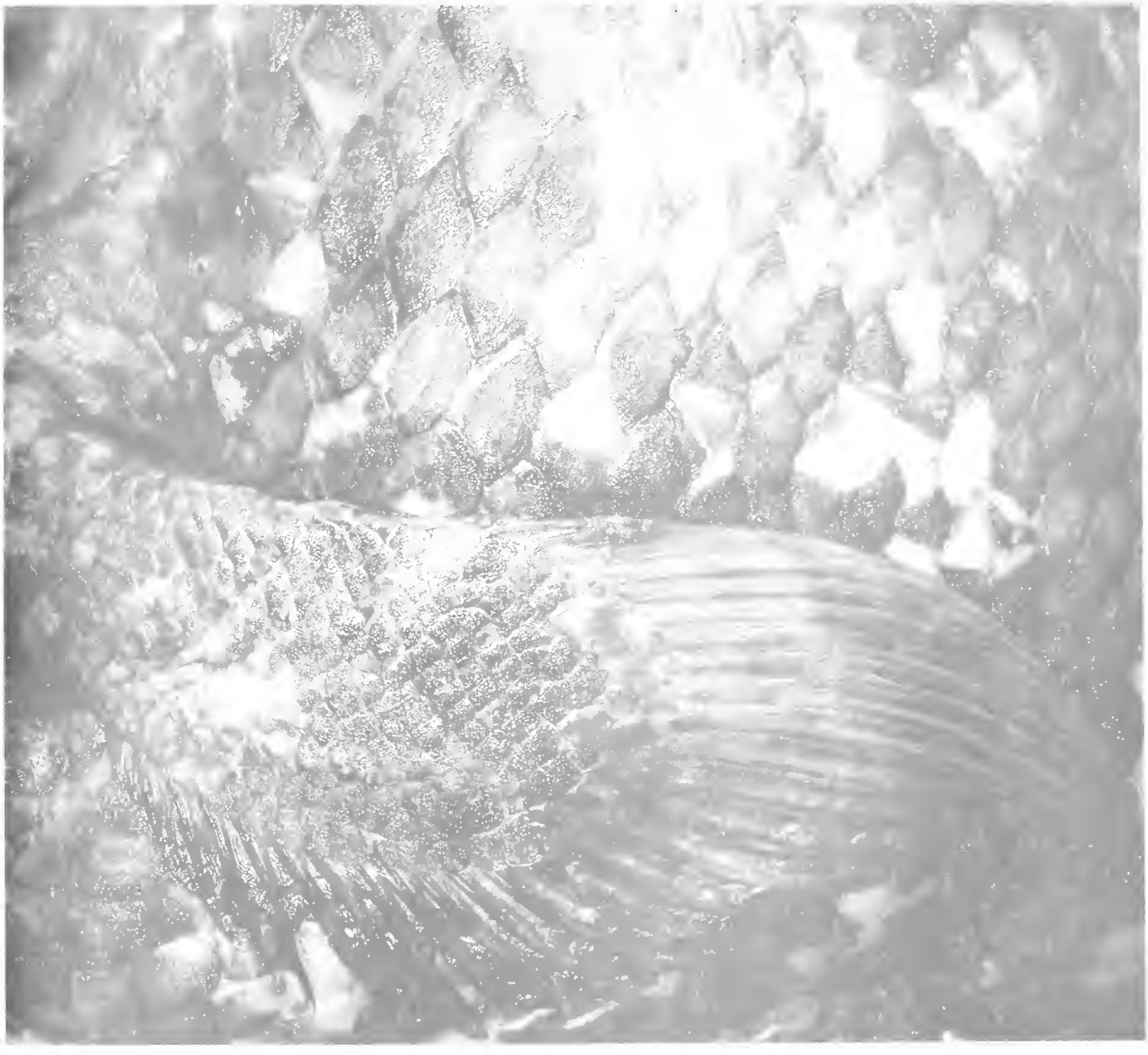

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SAIAB

Margaret Mary Smith (1916–1987),
James Leonard Brierley Smith (1897–1968)
with their dog Marlin

The publication series (Monographs, Bulletins) of SAIAB (formerly the JLB Smith Institute of Ichthyology), in its new format, honours James Leonard Brierley Smith and Margaret Mary Smith with the name *Smithiana*, in recognition of their many years of devoted service to African aquatic biology. Their life's work, a team effort, established modern ichthyology in southern Africa and laid the groundwork for the expansion of aquatic biology throughout the region.

CONTENTS

Smithiana Bulletins and Monographs are publications of the South African Institute for Aquatic Biodiversity, for original scientific articles in the fields of taxonomy, systematics, ethology, ecology, biogeography and conservation of the fishes of Africa and its surrounding waters. Priority will be given to papers by staff and associates of the Institute. Manuscripts from outside the Institute will be considered if they are pertinent to the work of the Institute or use the Institute's collections.

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Luthulenchelys heemstraorum, a new genus and species of snake eel (Anguilliformes: Ophichthidae) from KwaZulu-Natal, with comments on *Ophichthus rutidoderma* (Bleeker, 1853) and its synonyms

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Abstract. *Luthulenchelys heemstraorum* genus and species novum, subfamily Ophichthinae, tribe Ophichthini, is described from a 472 mm eel trawled off Durban, KwaZulu-Natal, South Africa, in 450–460 m. *Luthulenchelys* differs from all known ophichthids in having the following suite of characters: an extremely elongate body, long tail, dorsal-fin origin in anterior trunk region, an elongate pectoral fin, posterior eye/jaw location, blunt snout, posterior nostril within upper lip, slender dentition, a single vomerine tooth, uniquely developed lateral-line ossicles, and five gill arches, with a very reduced fifth ceratobranchial. Several changes in taxonomy are proposed: *Ophisurus lumbricoides* Bleeker 1853, *Ophisurus rutidodermatoides* Bleeker 1853, and *Ophichthus derbyensis* Whitley 1941 are junior synonyms of *Ophichthus rutidoderma* (Bleeker 1853); *Sphagebranchus lumbricoides* Bleeker 1864 is a species of *Yirrkala*.

Key Words: Ophichthidae, *Luthulenchelys heemstraorum* gen. & sp. nov., KwaZulu-Natal, South Africa, *Ophichthus rutidoderma*, *Ophichthus rutidodermatoides*, *Ophichthus derbyensis*, *Yirrkala lumbricoides*

INTRODUCTION

The snake eel fauna of the Western Indian Ocean is rich, diverse and poorly known. J.L.B. Smith (1962) included 55 species in his monograph of the Western Indian Ocean and Red Sea ophicthids. McCosker and Castle's (1986) account of the southern African species (from northern Namibia to Mozambique) treated 29 species and made several changes in taxonomy. In a forthcoming volume on coastal fishes of the Western Indian Ocean and Red Sea (Phillip Heemstra and Jack Randall, editors), I will report at least 70 species and 30 genera of ophichthids, including numerous changes in taxonomic status. In preparation for that work I have examined many of the recently collected specimens from South Africa and beyond that are deposited in the collections of the South African Institute for Aquatic Biology, the Bernice P. Bishop Museum, the United States National Museum of Natural History, the California Academy of Sciences, the British Museum of Natural History, and other institutions, and have discovered at least six species of ophichthids that appear to be undescribed, as well as a number of eels whose taxonomic history is as twisted as the state of their holotypes. Undoubtedly additional ophicthid species from this area remain to be discovered. The majority of the known undescribed species await description or explanation in a variety of generic revisions that are underway. One new species, however, is so distinct that it deserves a new genus as well, and in preparation for the publication of the Western Indian Ocean volume, I herein describe it and take pleasure in naming it after Phil and Elaine Heemstra in recognition of their prodigious efforts in this and previous regional works.

MATERIALS AND METHODS

The single specimen is deposited at the South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown.

Specimen measurements are straight-line, made either with a 300 mm ruler with 0.5 mm gradations (for total length, trunk length, and tail length) and recorded to the nearest 0.5 mm, or with dial calipers (all other measurements) and recorded to the nearest 0.1 mm. Body length comprises head and trunk lengths. Head length is measured from the snout tip to the postero-dorsal margin of the gill opening; trunk length is taken from the gill opening to mid-anus; maximum body depth does not include the median fins. Head-pore terminology follows McCosker et al. (1989: 257), in which supraorbital pores include the ethmoidal pore + pores in supraorbital canal, i.e. 1 + 3, and the infraorbital pores include pores along the upper jaw + those in the vertical canal behind the eye ("postorbital pores"), i.e. 4 + 2, as the last pore included along the upper jaw is frequently part of the postorbital series. Gill arch and lateral-line ossicle examination was accomplished after removal and clearing and counterstaining with alcian blue and alizarin red dyes (Dingerkus & Uhler 1977). Vertebral counts (which include the hypural) were taken from radiographs. Radiographic techniques are described in (Böhlke 1989). The mean vertebral formula (MVF) is expressed as the average of predorsal, preanal, and total vertebrae (Böhlke, 1982). Institutional abbreviations follow (Leviton et al., 1985).

Luthulenchelys gen. nov.

Figs. 1-4

Type species: *Luthulenchelys heemstraorum* sp. nov.

DIAGNOSIS. An elongate ophichthid, subfamily Ophichthinae, tribe Ophichthini (sensu McCosker 1977), with tail much longer than head and trunk; median fins low; dorsal fin arising well behind pectoral fin; pectoral fin base arising above and occupying more than half of gill opening; gill openings lateral, elongate, nearly vertical and crescentic; eye moderately developed, its centre above posterior quarter of upper jaw, its posterior margin slightly in advance of rictus; jaws moderately developed, but not elongate; snout conical, tapering evenly, its tip rounded; underside of snout with a median sulcus exposing the teeth in advance of anterior nostril bases; anterior nostrils within short tubes; posterior nostrils a hole within upper lip, covered by a flap; teeth conical, erect, numerous and small, uniserial on mandible and biserial on maxillary, a single vomerine tooth; 2 preopercular pores; gill arches similar to those of *Ophichthus* (cf. Nelson 1966; McCosker 1977), however, fifth ceratobranchial is a thin, nearly ossified rod for anterior 80%, the remainder cartilaginous; upper pharyngeal tooth plates fused. Other characters those of the single species.

ETYMOLOGY. Named *Luthulenchelys* in honour of Chief Albert John Mvumbi Luthuli of KwaZulu-Natal, Africa's first winner of the Nobel Peace Prize and former President of the African National Congress; and *enchelys*, an ancient Greek word for eel, feminine.

REMARKS. In general appearance, the type species of *Luthulenchelys* appears similar to some of the very elongate species of *Ophichthus*, such as *O. rutidoderma* and *O. microcephalus*. *Luthulenchelys heemstraorum* differs from them in the condition of its upper lip and associated posterior nostril, its large posterior eye (ending nearly above rictus, rather than in advance of it), its reduced vomerine dentition, its fifth ceratobranchial reduced to a minor cartilaginous rod (rather than an ossified structure), and in the condition of its lateral-line ossicles.

Adaptations displayed by the new species such as the nearly uniform dark coloration, small and numerous teeth, fairly large eye, tumid snout (associated with burrowing in soft mud, rather than the sharp-pointed snouts and tails of shallow-water ophichthids that are adaptations for burrowing into sand), moderately developed cephalic pores, and poorly developed median fins are shared by other deep-dwelling ophichthids (cf. McCosker et al. 1989; McCosker 1999). Those similarities and adaptations are so apparent that upon first glance the new species appears very similar to several deep-dwelling Atlantic myrophine ophichthids (McCosker, 1989), such as *Asarcenchelys longimanus* McCosker 1985, *Mixomyrophis pusillipinna* McCosker 1985 and *Pseudomyrophis nimius* Böhlke 1960, whose ancestry is very different to that of the new species.

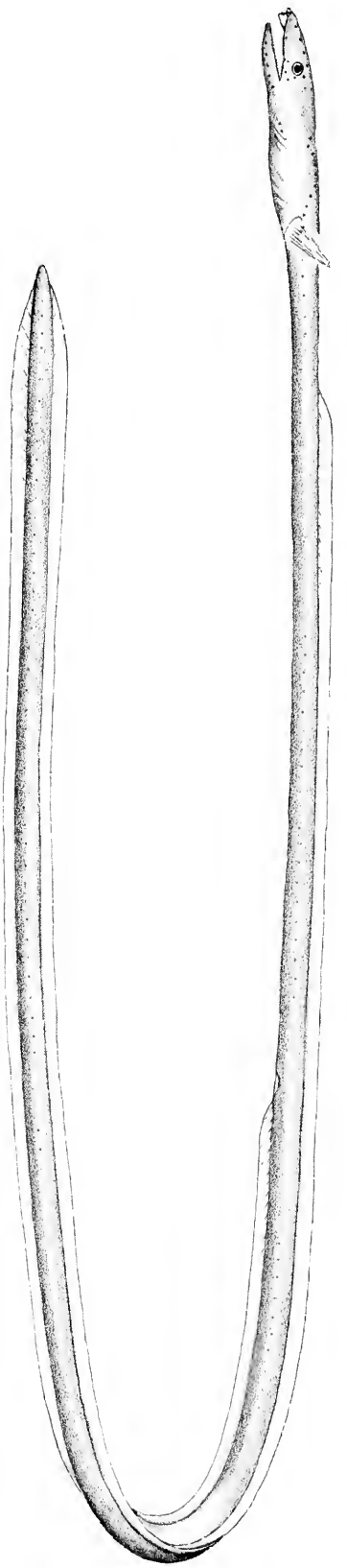

Fig. 1. Holotype of *Luthulenchelys heemstraorum* sp. nov., SAIAB 75732, 472 mm TL.

Luthulenchelys heemstraorum sp. nov.

Holotype: SAIAB 75732, 472 mm TL, sex undetermined (gonads not apparent), from KwaZulu-Natal, South Africa, off Durban (29°57′14″S, 31°16′23″E), 450–460 m, collected by Grant van der Westhuizen aboard F/V *Ocean Spray* using an otter trawl, field no. ORI 180-3/5, on 16 November 2004.

Diagnosis. An elongate species of ophichthine with: tail 62%, head 7.2%, and body depth at gill opening 1.3% of total length; dorsal-fin origin nearly 2 head lengths behind pectoral-fin tips; pectoral fin elongate; posterior nostril a hole within upper lip, covered by a flap that extends below edge of lip; no barbels on upper lip and a no slit at posterior nostril; pores small but conspicuous, SO 1 + 4, IO 4 + 2, POM 5 + 2; teeth small and conical, biserial on upper jaw, uniserial on lower jaw, a single vomerine tooth; coloration uniform grey-black; vertebral formula 20/61/165.

Counts and measurements of the holotype (in mm). Total length 472; head 34.0; trunk 144; tail 294; predorsal distance 64; pectoral-fin length 8.25; pectoral base 2.4; body depth ~6 at gill openings; body width ~6 at gill openings; body depth ~5 at anus; body width ~5 at anus; snout 7.5; tip of snout to rictus 11.2; snout overhang 3.5; eye diameter 3.0; interorbital width 3.5; gill opening height 3.1; isthmus width 2.6.

Description. Body very elongate, trunk subcircular, tail laterally compressed; body depth at gill openings 79 in TL. Branchial basket moderately expanded; 17 pairs of overlapping branchiostegal rays visible by radiograph. Head 4.2 in trunk. Head and trunk 2.7 and head 14 in TL. Snout rounded, moderately acute when viewed from above; a short groove bisecting underside of snout nearly to tip of upper jaw. A pair of small bumps on snout flanking dorsal midline in advance of anterior nostril base (their appearance possibly exaggerated by condition of specimen). Lower jaw included, its tip reaching well beyond base of anterior-nostril tubes. Upper jaw not elongated, rictus immediately behind a vertical line at posterior margin of eye. Eye fairly large, 3.7 in upper jaw and 11.3 in head. Anterior nostrils tubular, extending ventro-laterally from snout at ~45° from horizontal, reaching below upper lip and beyond tip of chin. Posterior nostrils an elongate opening within upper lip, not visible externally, covered by a flap (expanded edge of lip) that extends below edge of mouth and lacks a vertical slit. No barbels along upper lip. Dorsal-fin origin well behind pectoral fin about a head length into trunk length. Median fins low but obvious, ending a little more than eye diameter before bluntly pointed and laterally compressed tail tip. Pectoral fins elongate.

Head pores small but apparent (Fig. 2). Single median interorbital and temporal pores. Supraorbital pores 1 + 4, infraorbital pores 4 + 2, lower jaw pores 5, preopercular pores 2, supratemporal pores 3. Lateral-line pores apparent only in anterior trunk region; 9 before gill opening in a high-arching sequence, the remainder difficult to discern due to condition of specimen. Lateral-line canal unique in appearance (Fig. 3) among the Ophichthini, exhibiting horizontal tubes indented at each end; pores in tail region appear as prominent sharp spikes as seen from above (these are lateral processes of the vertebrae as evidenced by radiography, perhaps exaggerated by the desiccated condition of the specimen), reaching nearly to tail tip.

Fig. 2. Head of holotype of *Luthulenchelys heemstraorum* sp. nov., SAIAB 75732, 472 mm TL.

Fig. 3. Left lateral-line pores 21-23 of holotype of *Luthulenchelys heemstraorum* sp. nov., Scale indicates 1 mm.

Teeth (Fig. 4) small, conical, slightly recurved; biserial in upper jaw and uniserial on mandible. An intermaxillary rosette of 4, followed by a gap, then a diamond of 4, followed by a single vomerine teeth. Maxillary tooth rows linear, separated by a narrow gap; inner row of ~16–17 larger teeth, flanked medially by ~22–24 smaller teeth in outer row. Lower-jaw teeth uniserial, ~28–30 descending in size to become very small posteriorly.

Fig. 4. Dentition of holotype of *Luthulenchelys heemstraorum* sp. nov., SAIAB 75732, 472 mm TL.

Gill arches removed, cleared and counterstained. Gill arches developed, similar to those of *Ophichthus* (cf. McCosker 1977: 32) except for fifth ceratobranchial condition; first basibranchial ossified, all others cartilaginous; hypobranchials 1–2 ossified, 3–4 cartilaginous; epibranchials 1–4 ossified; infra-pharyngobranchials 2–3 ossified; fifth ceratobranchial very reduced, a thin nearly ossified rod for anterior 80%, the remainder cartilaginous; upper pharyngeal

tooth plates fused, containing 2–4 rows of conical recurved teeth; lower pharyngeal tooth plates contain 2–3 rows of 6–14 conical recurved teeth.

Colour in ethanol: uniform grey-black; throat, snout and chin slightly darker; median and pectoral fins pale; anterior nostrils, inside of mouth, anal region and peritoneum pale. A photograph of the dead specimen taken soon after its capture indicates that in life it was uniform dark brown.

ETYMOLOGY. Named in honour of Phil and Elaine Heemstra in recognition of their efforts to understand, illustrate, and explain the fishes of the Indian Ocean to scientists and the general public.

DISTRIBUTION. Known only from the type specimen, collected off Durban in 450–460 m depth.

REMARKS AND COMPARISONS. The characteristics of the new species are those of the monotypic genus. The new species is easily separable from any known ophichthid on the basis of its eye size and location, its extremely reduced vomerine dentition, its body elongation, and other characters unique to the genus. Comparisons with species of *Ophichthus* that are similar in appearance are described in the following section.

COMMENTS ON *OPHICHTHUS RUTIDODERMA*

During my initial attempts to identify the specimen herein described as *Luthulenchelys heemstraorum*, I examined the extremely elongate species of *Ophichthus*, *O. microcephalus* and *O. rutidoderma*. *Ophichthys microcephalus* Day 1878 was described from Malabar, India, and is currently known only from Day's description and an extant 625 mm TL syntype in the Australian Museum (B.7843). (*Ophichthus microcephalus* may ultimately deserve relocation to another genus, however, the extant syntype is somewhat desiccated and its head is damaged, which would disallow an adequate generic decision.) I compared that syntype to the holotype of *Luthulenchelys heemstraorum* and found them to differ in numerous characters: the teeth of *O. microcephalus* are more numerous, more closely-set, and stouter than those of *L. heemstraorum*; the snout is shorter and sharper, the body less elongate, the eye is comparatively smaller and located more anteriorly, and *O. microcephalus* has more vertebrae than *L. heemstraorum* (12/69/209 vs. 20/61/165); and its lateral-line ossicles are more typical of the *Ophichthus* condition (McCosker 1977) than are those of *L. heemstraorum*.

I also compared the shallow-water Indonesian species *Ophichthus rutidoderma* (Bleeker 1853) (treated by Kaup 1856: 18, as *Pisoodonophis rutidoderma*, later emended to *Ophichthys rhytidoderma* by Günther 1870: 63) to *Luthulenchelys heemstraorum*. It has a similar dorsal-fin origin (above the 16th vertebra) and biserial dentition, but the snout is shorter and sharper, its eye is smaller and located more anteriorly than that of *L. heemstraorum*, its lateral-line ossicles are more typical of the *Ophichthus* condition (McCosker 1977), and it has more total vertebrae (195-199 vs. 165).

While examining the type (BMNH 1867.11.28:226, 94.5 cm TL) of *Ophisurus rutidoderma* Bleeker (1853: 30) at the British Museum, I attempted to decipher its identity and that of related Bleeker types. I ultimately concluded that *Ophisurus rutidodermatoides* Bleeker (1853: 31) [treated by Kaup 1856: 18, as *Pisoodonophis rutidermatoides* (sic.), later emended to *Ophichthys rhytidodermatoides* by Günther 1870: 62] and *Ophisurus lumbricoides* Bleeker (1853: 32) are junior synonyms of *O. rutidoderma*. The types of *O. rutidodermatoides* (BMNH 1867.11.28:292, 61 cm TL) and *O. lumbricoides* (BMNH 1867.11.28:300, 41.5 cm TL) are in poor condition, however, that of *O. rutidoderma* is in fair condition. Eschmeyer (1998: 1491) cited *O. rutidoderma* and *O. rutidodermatoides* as valid species whose unique holotypes were "whereabouts unknown." My examination of those Bleeker specimens in the British Museum demonstrated that the length and locality data were appropriate, and I therefore identify those specimens, with confidence, as the holotypes. Eschmeyer (1998: 951) listed *O. lumbricoides* as a valid species of *Yirrkala*, and also suggested that the whereabouts of the unique holotype was unknown. It is in fact the British Museum specimen, as evidenced by the length of the specimen and additional records in the collection; Eschmeyer's assumption of its validity was based upon McCosker and Castle's (1986: 185) mistaken referral of *Ophisurus lumbricoides* Bleeker 1853, rather than *Sphagebranchus lumbricoides* Bleeker 1864, to *Yirrkala* in their treatment. I have also examined the holotype (AM.I.840, 258 mm TL) of *Ophichthus derbyensis* Whitley 1941 described from a specimen from Derby, Western Australia, and found it to be a synonym of *Ophichthus rutidoderma*. It has the same proportions, meristics, and dental condition as that of Bleeker's type specimens. The vertebral formulae of the four holotypes are as follows: *O. derbyensis* 14/61/195; *O. lumbricoides* 16/64/199; *O. rutidoderma* 16/61/197; and *O. rutidodermatoides* ?/63/197.

In summary, the twisted tale of these elongate ophichthids is as follows: *Ophisurus lumbricoides* Bleeker 1853, *Ophisurus rutidodermatoides* Bleeker 1853, and *Ophichthus derbyensis* Whitley 1941 are herein considered to be junior synonyms of *Ophichthus rutidoderma* (Bleeker 1853), and *Sphagebranchus lumbricoides* Bleeker 1864 is a valid species of *Yirrkala*.

ACKNOWLEDGEMENTS

My list of acknowledgments could easily exceed the length of the elongate holotype of the new species. I sincerely thank the following for their assistance: Grant van der Westhuizen and Sean Fennessy of the

South African Oceanographic Research Institute (ORI) for collecting and photographing the type specimen; Beth Herd Guy for preparing the illustrations; Mysi Hoang (CAS) for clearing and staining the gill arches and skin segment; William N. Eschmeyer (CAS) for advice concerning nomenclature; the research and curatorial staff members of the Australian Museum (AMS), the British Museum of Natural History (BMNH), the Bernice P. Bishop Museum (BPBM), the California Academy of Sciences (CAS), the South African Institute for Aquatic Biodiversity (SAIAB), the United States National Museum of Natural History (USNM), and the Universiteit van Amsterdam Zoologisch Museum (ZMA) for their assistance with specimens; Phil Heemstra and the late Margaret Mary Smith for their advice and assistance during my visits to SAIAB; Tomio Iwamoto (CAS) for reading a draft of this manuscript; and Don Linker and the Jewish Community Endowment Fund for their financial support of the artist.

LITERATURE CITED

BLEEKER, P. 1853. Bijdrage tot de kennis der Muraenoïden en Symbranchoïden van den Indischen Archipel. *Verhandelingen van het Bataviaasch Genootschap van Kunsten en Wetenschappen* **25**: 1–76.

— 1864. *Atlas ichthyologique des Indes Orientales Néêrlandaises, publié sous les auspices du gouvernement colonial.* Tome 4, Murénes, Synbranches, Leptocéphales. Leiden. 132 pp, plates 145–193.

BÖHLKE, E. B. 1982. Vertebral formulae of type specimens of eels (Pisces: Anguilliformes). *Proceedings of the Academy of Natural Sciences of Philadelphia* **134**: 31–49.

— 1989. Methods and Terminology. In: Fishes of the Western North Atlantic, Part 9, Volume 1, ed. E.B. Böhlke, pp. 1–7. *Memoirs of the Sears Foundation for Marine Research*, New Haven.

BÖHLKE, J.E. 1960. A new ophichthid eel of the genus Pseudomyrophis from the Gulf of Mexico. *Notulae Naturae* No. 329: 1–8.

DAY, F. 1878. *The fishes of India; being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon.* Part **4**: 553–779.

DINGERKUS, G. & L.D. UHLER. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technology* **52**: 229–232.

ESCHMEYER, W. N., ed. 1998. *Catalog of Fishes.* California Academy of Sciences, San Francisco. 3 vols., 2905 pp.

GÜNTHER, A. 1870. Catalogue of the Physostomi, containing the families Gymnotidae ... Leptocardii, in the British Museum. *Catalogue of the fishes in the British Museum.* Vol. 8. British Museum, London. 549 pp.

KAUP, J. 1856. *Catalogue of apodal fish in the collection of the British Museum.* London. 160 pp.

LEVITON, A.E., R.H. GIBBS, JR., E. HEAL & C.E. DAWSON. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resources collections in herpetology and ichthyology. *Copeia* **1985**: 802–832.

MCCOSKER, J.E. 1977. The osteology, classification, and relationships of the eel family Ophichthidae. *Proceedings of the California Academy of Sciences* ser. 4, **41**(1): 1–123.

— 1985. Two new genera and two new species of deepwater western Atlantic worm eels (Pisces: Ophichthidae). *Proceedings of the California Academy of Sciences* **44**(2): 9–15.

— 1999. Pisces Anguilliformes: Deepwater snake eels (Ophichthidae) from the New Caledonia region, Southwest Pacific Ocean. In: A. Crosnier (ed.), *Résultats des Campagnes MUSORSTOM Vol. 20*, ed. A. Crosnier. *Mémoires du Muséum national d'Histoire naturelle* **180**: 571–588.

MCCOSKER, J.E., E.B. BÖHLKE & J.E. BÖHLKE. 1989. Family Ophichthidae. In: Fishes of the Western North Atlantic, Part 9, Volume 1, ed. E.B. Böhlke, pp. 254–412. *Memoirs of the Sears Foundation for Marine Research*, New Haven.

MCCOSKER R, J.E. & P.H.J. CASTLE. 1986. Family Ophichthidae. *In*: Smith, M.M. and P.C. Heemstra (eds.), *The Sea Fishes of Southern Africa*, pp. 176–186. Macmillan South Africa, Johannesburg.

NELSON, G.J. 1966. Gill arches of teleostean fishes of the order Anguilliformes. *Pacific Science* **20**(4): 391–408.

SMITH, J.L.B. 1962. Sand-dwelling eels of the western Indian Ocean and the Red Sea. *Rhodes University Ichthyological Bulletin* **24**: 447–466.

WHITLEY, G.P. 1941. Ichthyological notes and illustrations. *Australian Zoologist* **10**: 1–50.

Iniistius griffithsi, a new razorfish (Perciformes: Labridae) from Mauritius

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Abstract. The razorfish *Iniistius griffithsi* is described from three male specimens caught by handline off the south coast of Mauritius in 120 m. It is distinct in lacking scales on the cheek except for a curved row of 6 small scales from behind to below the eye; 19–20 gill rakers; body depth of 2.5–2.6 in standard length; first two dorsal spines slender, flexible, and not long (the first 2.45–2.55 in head length); space between first and second dorsal spines more than twice that between second and third spines; and in colour. The most conspicuous colour markings are a broad oblique pale blue band containing many small black spots from high on the nape to above the opercle, and black spots of about pupil size, each edged in pale blue, on the side of the body above the tip of the pectoral fin.

Key words: Taxonomy, Labridae, *Iniistius griffithsi* sp. nov., Mauritius

INTRODUCTION

Labrid fishes of the six genera of the subfamily Xyrichtyinae (Hemipteronotinae of Norman 1957) contain species that are able to escape predation by quickly diving into sand: *Ammolabrus, Cymolutes, Iniistius, Novaculichthys, Novaculoides* and *Xyrichtys*. Three of the genera are monotypic: *Ammolabrus dicrus* Randall & Carlson is a zooplankton feeder that forms aggregations over open sand substrata; *Novaculichthys taeniourus* (Lacepéde) is usually seen over sand and rubble areas near reefs; and *Novaculoides macrolepidotus* (Bloch) typically hides in seagrass or algal beds, which it resembles in its colouration. The species of the other three genera may be found over broad open stretches of sand far from the shelter of reefs or dense plant growth needed for shelter by other benthic shore fishes. The three species of *Cymolutes* have been given the common name knifefishes, and those of *Xyrichtys* and *Iniistius* are called razorfishes, in both cases alluding to their compressed bodies and the sharp leading edge of their forehead and snout, specialisations for quick entry into sand.

Some razorfishes have been classified in the genus *Hemipteronotus* Lacepéde. As recommended by Randall & Bauchot (1993), this generic name was suppressed by Opinion 1799 of the International Commission on Zoological Nomenclature to preserve the names *Naucrates* and *Xyrichtys*.

Iniistius has been considered as a synonym of *Xyrichtys* by some authors. Randall & Earle (2002) followed Tri-thuc Nguyen (1974) who differentiated the two genera osteologically. Externally, the two genera can be distinguished by three characters of the dorsal fin: the origin of the fin is over or less than half an orbit diameter behind the eye in *Iniistius*, but an eye diameter or more behind the eye in *Xyrichtys*. The first two dorsal spines of Iniistius are flexible, whereas only the first is flexible in *Xyrichtys*. The space between the second and third dorsal spines in *Iniistius* is much broader than the space between the third and fourth spines; by contrast these two spaces are about equal in *Xyrichtys*. Randall & Earle provided a diagnosis of *Iniistius*.

Species of *Xyrichtys* occur in the Atlantic, eastern Pacific and the Indo-Pacific region, whereas those of *Iniistius* are confined to the Indo-Pacific, except *I. pavo* (Valenciennes), which has extended its range to the eastern Pacific. As might be expected from their habits, razorfishes are not well represented in museum collections. One is described here in the genus *Iniistius* from three specimens from Mauritius.

MATERIALS AND METHODS

Type specimens are deposited in the Australian Museum, Sydney (AMS); Bernice P. Bishop Museum, Honolulu (BPBM); and U.S. National Museum of Natural History, Washington, D.C. (USNM).

The length of specimens is given as standard length (SL), measured from the median anterior end of the upper lip to the base of the caudal fin (posterior end of the hypural plate); body depth is the greatest depth from the base of the dorsal spines to ventral edge of the abdomen (correcting for any malformation of preservation); body width is measured just posterior to the gill opening; head length is taken from the upper lip to the posterior end of the opercular flap; orbit diameter is the greatest fleshy diameter, and interorbital width the least bony width; snout length is measured from the median anterior point of the upper lip to the nearest fleshy edge of the orbit; upper-jaw length from the same anterior point to the posterior end of the maxilla; caudal-peduncle depth is the least

depth, and caudal-peduncle length the horizontal distance between verticals at the rear base of the anal fin and the caudal-fin base; lengths of spines and rays are measured to their extreme bases; caudal-fin and pectoral-fin lengths are the length of the longest ray; pelvic-fin length is measured from the base of the pelvic spine to the tip of the longest soft ray.

Morphometric data are presented in Table 1 as percentages of the standard length. Proportional measurements in the text are rounded to the nearest 0.05.

Lateral-line scale counts include the last pored scale that overlaps the end of the hypural plate; scales in transverse series are counted from the origin of the anal fin obliquely upward to the base of the first dorsal fin; the count of gill rakers is made on the first gill arch and includes all rudiments.

Meristic and morphometric data in parentheses refer to paratypes.

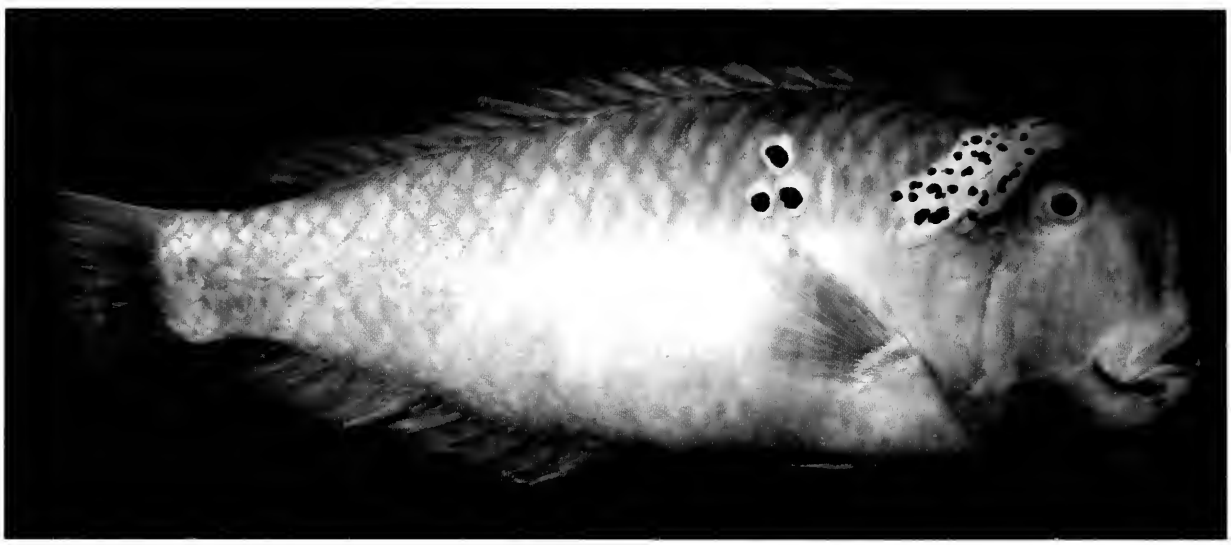

Fig. 1. Holotype of *Iniistius griffithsi*, BPBM 40486, male, 140 mm SL, Mauritius, 120 m (photograph by D. Lebreton).

Iniistius griffithsi, sp. nov.
(Figs. 1–3; Table 1)

Holotype: BPBM 40486, male, 140 mm SL, Mauritius, south coast, 0.5 km south of mouth of Rivière des Anguilles, about 1 km offshore from point at 20°31.2'S, 57°33'E, 120 m, handline, Jeremy Griffiths and Tonio Isidore, 1 May 2006.

Paratypes: AMS I.43854-001, male, 138 mm and USNM 388078, male, 143 mm, same data as holotype, except March, 2006.

DIAGNOSIS. Dorsal rays IX,12; anal rays III,12; pectoral rays 12; lateral line interrupted, the pored scales 19–20 + 5 or 6; cheek naked except for a curved oblique row of 6 small scales from behind to below eye; 1 or 2 small scales dorsoanteriorly on opercle; gill rakers 19-20; body depth 2.5–2.6 in SL; dorsal profile of snout nearly vertical; first two dorsal spines slender and flexible, the first slightly longer, 2.45–2.55 in head length; space between second and third dorsal spines more than twice that between first and second spines; colour when fresh, pale grey, scale edges dorsally on body grey-brown; head grey-brown, operculum suffused with orange, with vertical blue bands; a broad oblique pale blue band containing numerous small black spots from interorbital space to above opercle; one to several black spots, edged in pale blue, on side of body above tip of pectoral fin; a dusky streak below posterior end of maxilla and lower lip; orangish patch on side of caudal peduncle, each scale with a pale blue spot; median fins bluish grey; pectoral fins orange.

DESCRIPTION. Dorsal rays IX,12, all soft rays branched (first 4 or 5 rays of paratypes unbranched), the last to base; anal rays III,12, all branched (first ray of one paratype unbranched), the last to base; pectoral rays 12, the uppermost very short and spine-like, the second unbranched; pelvic rays I,5, all soft rays branched; principal caudal rays 12, the uppermost unbranched; upper procurrent caudal rays 6; lower procurrent caudal rays 5; lateral-line scales 20 + 5 (19–20 + 5–6), the last on base of caudal fin; scales above lateral line to origin of dorsal fin 4; scales above lateral line to middle of spinous portion of dorsal fin 2 (uppermost small); scales below lateral line to origin of anal fin 9; circumpeduncular scales 14; gill rakers 20 (19–20); branchiostegal rays 5; vertebrae 25.

Body deep, the depth 2.55 (2.5–2.6) in SL; body very compressed, the width 2.8 (2.75) in body depth; head length 2.9 (2.9–2.95) in SL; snout length (as measured from lower edge of orbit to front of upper lip) 1.9

(1.85–1.9) in head length; dorsal profile of snout nearly vertical to level of lower edge of eye, then convex to above eye (indentation of profile above upper lip of holotype the result of a wound, probably from the hook); front of snout narrowing to sharp ridge that extends to above eye; front of chin also a ridge though not as sharp as that of snout; eye set high on head, but nearly an orbit diameter vertically below dorsal profile of interorbital space; orbit diameter 6.0 (5.9-6.2) in head length; interorbital width 5.45 (5.4-5.5) in head length; caudal-peduncle depth 2.6 (2.5-2.75) in head length; caudal-peduncle length 4.05 (3.9-4.0) in head length.

Mouth moderately large, the maxilla extending to or nearly to a vertical at anterior edge of orbit, the upper-jaw length 2.8 (2.75–2.85) in head length; mouth slightly oblique, forming an angle of about 20° to horizontal axis of body; a pair of large, recurved, outflaring canine teeth at front of jaws that overlap lips when mouth closed, the lower pair medial to upper; side of jaws with a close-set series of strong conical teeth, 14 on upper jaw and 13 in lower jaw of holotype; two to three irregular rows of small, slightly nodular teeth medial to row of conical teeth in upper jaw, and one to two rows in lower jaw. Tongue broadly rounded, set far back in mouth. Lips thin, the lower with a well-developed flap along side of mandible. Gill rakers short, the longest on first arch about one-half length of longest gill filaments.

Posterior edge of preopercle free nearly an eye diameter below ventral edge of orbit, the ventral edge nearly or just reaching a vertical at posterior edge of maxilla; a narrow fleshy flap surrounding orbit from below anterior edge of pupil to above posterior edge of pupil. Nostrils very small, before lower fourth of eye, the anterior two-thirds orbit diameter before eye, pore-like with a short rim and dorsoposterior flap; posterior nostril a short, near-horizontal slit dorsoposterior to anterior nostril, the internarial space nearly one-half pupil diameter. Cephalic sensory pores tiny; sub-orbital pores 6, with 2 isolated pores one above the other, nearly an orbit diameter below front edge of eye; a series of 8 preopercular pores, continuing anteriorly as 3 mandibular pores.

Scales cycloid and very thin; lateral-line scales with a single horizontal tubule, ending posteriorly in a pore; scales on chest about half height of largest scales on side of body; head naked except for one or two small scales dorsally on opercle and a curved series of six scales, progressively smaller ventrally from behind lower part of eye to below posterior edge of pupil (paratypes with two or three small partially embedded scales ventral to lowermost scale in oblique row); no scales on dorsal and anal fins; two or three rows of scales basally on caudal fin; no pelvic axillary scale; a single scale extending posteriorly from between base of pelvic fins, its length about equal to half length of pelvic spine.

Origin of dorsal fin above posterior edge of orbit, the predorsal length 3.6 in SL; first two dorsal spines slender and flexible, the remaining spines sharp-pointed and stiff; space between second and third dorsal spines more than twice space between first two spines; membrane deeply notched between second and third spines; first dorsal spine longest, slightly longer than second, 2.55 (2.45) in head length; third dorsal spine 4.85 (4.7–4.75) in head length: remaining dorsal spines progressively longer, the ninth 3.95 (3.95–4.05) in head length; fifth and sixth dorsal rays longest, 2.5 (2.55–2.6) in head length; origin of anal fin below base of first dorsal soft ray, the preanal length 1.85 (1.85–1.9) in SL; third anal spine longest, 4.35 (4.15–4.2) in head length; fifth anal soft ray longest, 2.6 (2.6–2.7) in head length; caudal fin slightly rounded, 4.85 (4.65) in SL; third and fourth pectoral rays longest, reaching to above origin of anal fin, 4.15 (3.85–3.9) in SL (distal end of about upper fourth of pectoral fin of right side of holotype missing); pelvic fins nearly or just reaching anus, the first soft ray longest, 5.15 (4.8–5.0) in SL; pelvic spine 2.25 (2.2–2.25) in length of longest pelvic soft ray.

Table 1. Proportional measurements of type specimens of *Iniistius griffithsi* as percentages of standard length (SL).

	Holotype	Paratypes	
	BPBM 40486	AMS I. 43854	USNM 388078
Standard length (mm)	140	138	143
Body depth	39.1	39.8	38.5
Body width	13.9	14.4	14.0
Head length	34.3	34.1	34.6
Snout length	18.3	18.2	18.2
Orbit diameter	5.7	5.8	5.6
Interorbital width	6.3	6.3	6.3
Upper-jaw length	12.2	12.4	12.2
Caudal-peduncle depth	13.3	13.6	12.6
Caudal-peduncle length	8.5	8.6	8.9
Predorsal length	27.8	28.0	27.8
Preanal length	53.8	52.5	54.2
Prepelvic length	31.3	31.0	31.9
Base of dorsal fin	74.4	76.1	74.5
First dorsal spine	13.5	13.8	14.0
Second dorsal spine	12.4	11.9	12.7
Third dorsal spine	7.1	7.2	7.4
Ninth dorsal spine	8.7	8.6	8.5
Longest dorsal ray	13.6	13.3	13.2
Base of anal fin	40.8	41.7	41.3
First anal spine	4.1	4.1	4.2
Second anal spine	5.8	6.6	6.3
Third anal spine	7.9	8.1	8.3
Longest anal ray	13.3	12.7	13.2
Caudal-fin length	20.7	21.4	21.6
Pectoral-fin length	24.2	25.8	25.9
Pelvic-spine length	8.7	9.2	9.0
Pelvic-fin length	19.5	20.8	20.0

Colour of holotype in alcohol: head, chest and most of abdomen purplish grey; body above lateral line dull greyish orange; broad middle zone of body yellowish white with a narrow midlateral dull orange stripe along middle of scale row; three black spots the size of pupil forming a triangle on side of body above distal end of pectoral fin, the uppermost spot on seventh lateral-line scale; scales on posterior fourth of body and base of caudal fin purplish grey, the scale edges paler; a broad oblique whitish band containing numerous small black spots of variable size from above eye, passing above operculum to level of lower edge of eye; lips and chin pale with a grey streak below ventral flap of lower lip to end of maxilla; dorsal and caudal fins translucent grey; anal and paired fins pale yellowish.

Colour of holotype when fresh as shown in Fig. 1. One of the paratypes has only a single pupil-size black spot below the seventh lateral-line scale and no others below. The other has black spots on nine scales, including sixth and seventh lateral-line scales of left side and sixth scale of right side, with one spotted scale above and six or seven on the two scale rows below. In addition, the second paratype has an isolated scale on one side below outer part of pectoral fin with two black spots. All of these spots were edged in pale blue in the newly caught fish. It is regretted that no female specimens were obtained. In view of the sexual dichromatism known for the species of *Iniistius*, the female can be expected to exhibit some difference in colour pattern. Juveniles will probably have still another pattern, most likely one with dark bars.

ETYMOLOGY. This species is named for the collector, Jeremy Griffiths.

REMARKS. The three specimens of *Iniistius griffithsi* were caught by handline from 120 m, hence deeper than normal scuba-diving depths. Fishes of this genus are highly esteemed as food fishes in spite of their relatively small size. They are often consumed by the fishermen themselves, therefore not often found in markets.

Two specimens of *Iniistius pavo* (Valenciennes) were caught from the same location and depth as the three of *I. griffithsi*. *Iniistius pavo* and the western Pacific *I. dea* (Temminck & Schlegel) are easily distinguished from all other species of the genus by the much longer and more forward position of the first two dorsal spines and their complete separation from the remaining spinous portion of the fin.

As noted by Randall et al. (2002), the remaining species of the genus *Iniistius* are divisible into two lineages, one with a broad band of scales that extend ventrally from below the eye to at least the level of the corner of the mouth, and other with just a few scales below the eye. *Iniistius griffithsi* falls in the latter group for which only *I. aneitensis* (Günther) and *I. cyanifrons* (Valenciennes) are known. It is easily distinguished from these two species by its striking black-spotted pattern.

ACKNOWLEDGEMENTS

I am most grateful to Owen Griffiths in Mauritius for noting that this species is an unusual fish, arranging for the collection of an additional specimen, and for its photograph by Dominique Lebreton. When informed of the plan to describe the fish in his honour, he asked that it be named for his son Jeremy, one of the two fishermen who caught the type specimens. Griffiths' first two specimens were given to the Australian Museum; Mark A. McGrouther kindly passed them on loan to me. Thanks are also due Loreen R. O'Hara for taking x-rays.

LITERATURE CITED

NGUYEN, T. 1974. Osteological studies on the labrid fishes (Family Labridae) of Japan-Morphology, taxonomy and phylogeny. Unpublished PhD thesis, Ocean Research Institute, University of Tokyo.

NORMAN, J. R. 1957. A draft synopsis of the orders, families and genera of Recent fishes and fish-like vertebrates. Trustees of the British Museum (Natural History), London.

RANDALL, J. E. & M. L. BAUCHOT. 1993. Case 2843. *Naucrates* Rafinesque, 1810 and *Xyrichtys* Cuvier, 1814 (Osteichthyes, Perciformes): Proposed conservation. *Bulletin of Zoological Nomenclature* **50**(4): 277–281.

RANDALL, J. E. & J. L. EARLE. 2002. Review of Hawaiian razorfishes of the genus *Iniistius* (Perciformes: Labridae). *Pacific Science* **56**(4): 389–402.

RANDALL, J. E., D. R. ROBERTSON & J. L. EARLE. 2002. *Iniistius auropunctatus*, a new razorfish (Perciformes: Labridae) from the Marquesas Islands. *Cybium* **26**(2): 93–98.

ADDENDUM

While this paper was in press, the author determined that Gerald R. Allen observed about 10 individuals of *Iniistius griffithsi* varying from about 8–18 cm in total length in the outer section of Loky Bay, northeastern Madagascar (12°43.532'S, 49°42.386'E) on a clean sand bottom at a depth of 8 m in March 2006. His underwater photographs of two adult individuals are reproduced here as Figs. 2 and 3. Allen observed a similar fish at Christmas Island in the Indian Ocean in July, 2006.

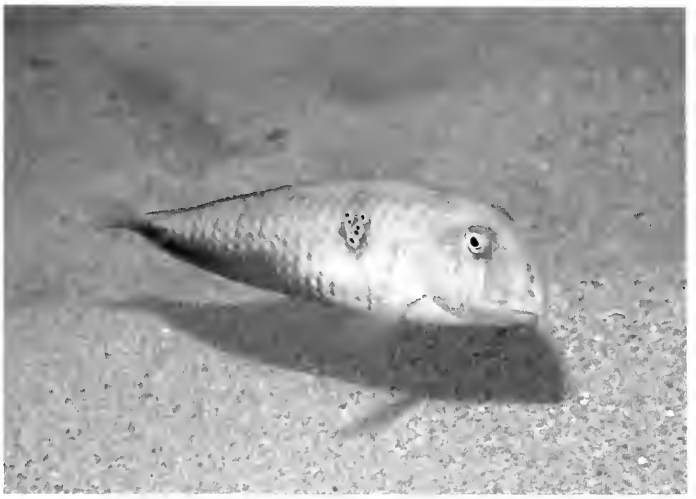

Fig. 2. *Iniistius griffithsi*, presumed female, Loky Bay, northern Madagascar (photograph by G.R. Allen).

Fig. 3. *Iniistius griffithsi*, presumed male, same locality as Fig. 2 (photograph by G.R. Allen).

Electrolux addisoni, a new genus and species of electric ray from the east coast of South Africa (Rajiformes: Torpedinoidei: Narkidae), with a review of torpedinoid taxonomy

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ABSTRACT. A new genus and species of sleeper ray, *Electrolux addisoni* (Family Narkidae), with two dorsal fins is described from two adult males (total lengths 50 and 52 cm) caught on a shallow reef off the east coast of South Africa. *Electrolux* is distinguished from other genera of Narkidae by its prominent spiracular papillae, the morphology of its nostrils, nasal curtain, mouth, jaws, chondrocranium, basibranchial skeleton, pectoral and pelvic girdles, and unique and complex colour pattern. It has higher vertebral, pectoral radial, tooth and intestinal valve counts than other narkids and reaches a greater size than all species with the possibly exception of *Typhlonarke aysoni*. Taxonomic definitions are provided for the electric rays, for the family Narkidae, and for Electrolux, as well as keys to families of electric rays and to the genera of Narkidae. The systematics of the narkid genus Heteronarce is reviewed and the genus validated. Members of the Narkidae may include the smallest, or at least the shortest, living chondrichthyans (*Temera hardwickii* and an undescribed species of *Narke*). *Electrolux addisoni* is a reef-dweller that eats polychaete worms and small crustaceans, and has been photographed and videotaped by divers while actively feeding in the daytime. The conspicuous dorsal colour pattern may be aposematic, as the ray was seen to make a possible threat display when closely approached. *Electrolux addisoni* is recorded from four localities along an approximately 310 km. strip of coastline from Coffee Bay, Eastern Cape Province, to just north of Durban, kwaZulu-Natal inside the 50 m isobath. This conspicuous, active ray is known only from a few diver records from reefs reported over approximately two decades, and its conservation status needs to be critically assessed.

KEY WORDS: *Electrolux addisoni*, new genus and species, Narkidae, sleeper ray, Torpedinoidei, description, taxonomy, distribution, biology, conservation status.

The coastal fish fauna of the east coast of South Africa is a mixture of tropical and subtropical Indo-West Pacific fishes (mainly coral-reef species), many endemic warm temperate species, and several worldwide species. This South African fish diversity is not well known, and in the past 20 years, our cursory fish survey work has produced numerous range extensions, many new records and several new species. In addition to our own collecting efforts and those of fisheries biologists on South African research vessels (particularly RV *Africana*; see Compagno, 1999b) and fishing companies and observers on fishing vessels, our knowledge of the South African marine fish diversity is significantly enhanced by the specimens and photographs provided by various amateur ichthyologists (anglers, aquarists, divers and underwater photographers).

This paper describes a remarkable new genus and species of electric ray (Family Narkidae) from the east coast of South Africa. The species was first made known to us by diver-photographer Peter Chrystal (through Rudy van der Elst, *pers. comm.*), who photographed this spectacular ray on a patch of sand on Aliwal Shoal, kwaZulu-Natal, South Africa in 1984 (Figure 1). The ray was subsequently rediscovered on Protea Banks off Shelly Beach, kwaZulu-Natal in 1997 by underwater photographers Stephania and Peter Lamberti (*pers. comm.*) who sent us a video-clip of the ray (Figure 2). It has also been photographed underwater at the Tee Barge north of Durban by Dennis King. A live specimen was seen underwater by P. Heemstra at Coffee Bay, Eastern Cape in 2001, but the ray fled before he could net it.

From the 1984 photographs we immediately recognized an undescribed species of electric ray (Torpedinoidei or Torpediniformes) with a unique dorsal colour pattern that was far more elaborate and ornate than that of any electric ray known at the time, although Last & Stevens (1994) and de Carvalho (1999) subsequently described species of *Narcine* off Australia and in the Western Hemisphere with ornate but simpler colour patterns. The ray was tentatively considered as either a member of the family Narkidae or Narcinidae by Compagno (in Smith & Heemstra, 1995) but after video footage became available, Compagno (1999b) thought it to be an undescribed narkid most probably of the genus *Heteronarce* because of its general morphology and twin dorsal fins.

However, the ray frustrated us by eluding capture for nearly two decades despite efforts by colleagues to collect it. In September 2003 a specimen (**SAIAB** 78777) was collected by Mark Addison on a reef off Manaba Beach near Margate in southern KwaZulu-Natal. A second specimen was collected by Mark's father, Brent Addison at the same locality in October 2003. Both specimens (Figures 3-4) were presented by Mark Addison to the South African Institute of Aquatic Biodiversity and the second specimen was transferred to the fish collection of Iziko - South African Museum (**SAM** 36908).

Study (including radiography) of the two specimens and dissection of the paratype (**SAM** 36908) confirmed our hypothesis that they represented a new species of the Family Narkidae (sleeper rays), which in South African waters also includes the common onefin electric ray, *Narke capensis* and the rare Natal electric ray, *Heteronarce garmani* (Compagno in Smith & Heemstra, 1986, Compagno et al., 1989). However, this new electric ray proved sufficiently different from known narkid genera *Heteronarke, Narke, Temera* and *Typhlonarke* to warrant a new genus and species (Compagno, 2005). We also discuss the systematics of *Heteronarce* and the Family Narkidae, and the taxonomy of electric rays, and comment on the size of narkid rays and the biology, habitat and conservation status of the new ray.

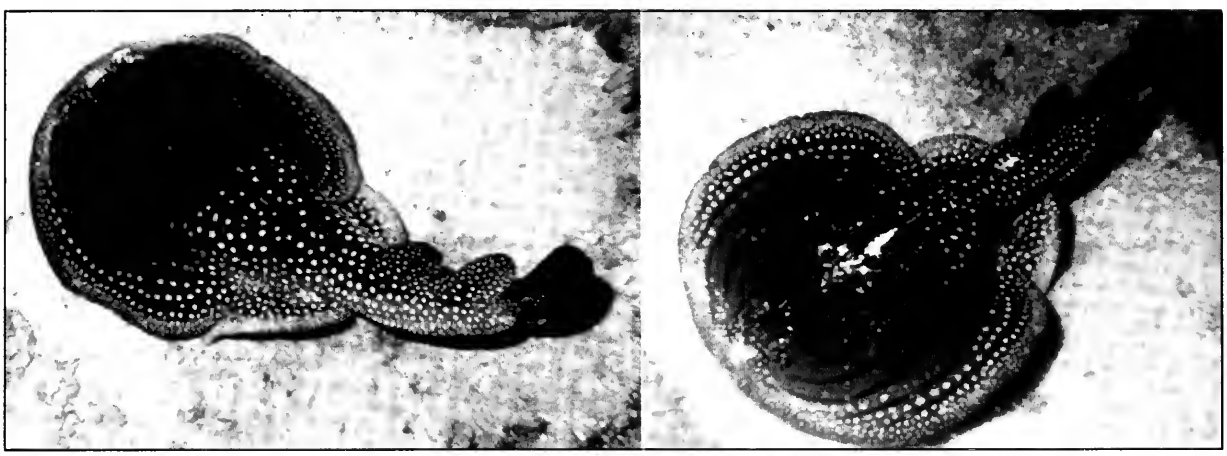

Figure 1. *Electrolux addisoni* photographed by Peter Chrystal at Aliwal Shoal, KwaZulu-Natal, South Africa in 1984. These two photographs were sent to the junior author by Rudy van der Elst and show the intricate concentric black stripe of the dorsal colour pattern on the disc of a live ray.

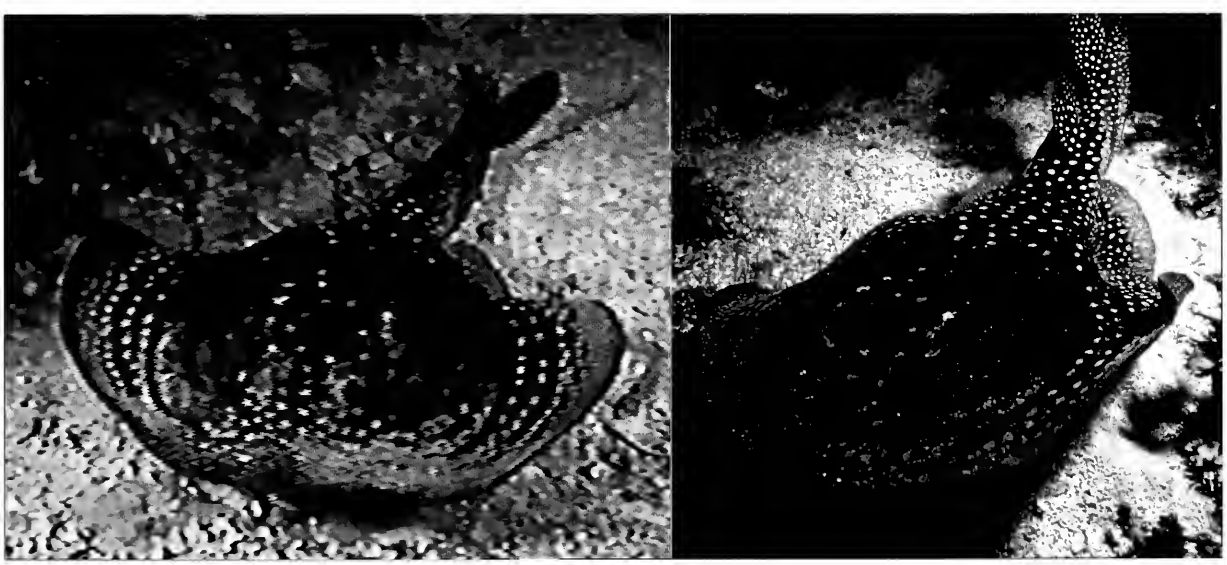

Figure 2. Two frames from a videotape of *Electrolux addisoni* taken by Stephania and Peter Lamberti in 1997 on Protea Banks off Shelly Beach, KwaZulu-Natal, South Africa. Left, ray vigorously feeding on substrate and moving towards the photographer, using its pelvic fins as legs. Right, ray stationary and giving a possible threat display, with disc curled and tail raised.

METHODS

EXTERNAL MORPHOLOGY AND MORPHOMETRICS: Terminology and abbreviations for torpedinoid external morphology and morphometrics are based on Bigelow and Schroeder (1953) for batoids, Compagno & Roberts (1982, 1984) for stingrays, and Compagno (1984, 1988, 2001) and Compagno *et al.* (2005) for sharks. Measurements and their abbreviations for electric rays are based on the system for sharks in Compagno (1984, 2001) with some modifications and additions. For the bases of precaudal fins the term **origin** is used for the anterior end of the fin base and **insertion for** the posterior end of the base. The morphometric abbreviations and definitions for torpedinoid measurements are presented below (Table 1). **Meristics**. Terminology and abbreviations for torpedinoid vertebral counts is derived from that for sharks in Compagno (1988) and for stingrays in Compagno & Roberts (1982, 1984) and are defined as follows: **SYN**, total synarcual vertebrae; sum of **SYC**, synarcual segments anterior to synarcual centra and determined by count of neural canals through lateral walls of synarcual, and **SYC**, synarcual centra in posterior end of synarcual. **MP**, monospondylous precaudal centra, between posterior end of synarcual and monospondylous-diplospondylous transition, sum of **MPN**, monospondylous precaudal centra without ribs, and **MPR**, monospondylous precaudal centra with ribs. **DP**, diplospondylous precaudal centra, between MP-DP transition and upper origin of caudal fin; sum of **DPN**, diplospondylous precaudal centra without ribs, and **DPR**, diplospondylous precaudal centra with ribs. **DC**, diplospondylous caudal centra from upper origin of caudal fin to end of vertebral column. **PC**, precaudal vertebrae, including **SYN**, **MP**, and **DP** vertebrae. **PCC**, precaudal centra, including **SYC**, **MP**, and **DP** centra. **TF**, total free centra from posterior end of synarcual to end of caudal centra; sum of **MP**, **DP**, and **DC** centra. **TC**, total free centra plus synarcual centra; sum of **SYC**, **MP**, **DP**, and **DC**. **TS**, total segments, all centra plus **SYS**. **SYN%**, total synarcual centra as percentage of total free centra, 100*(**SYN/TC**). **MP%**, monospondylous precaudal centra as percentage of total free centra, 100*(**MP/TC**). **DP%**, diplospondylous precaudal centra as percentage of total free centra, 100*(**DP/TC**). **DC%**, diplospondylous caudal centra as percentage of total free centra, 100*(**DC/TC**).

Tooth and intestinal valve terminology and count methodology is after Compagno (1988).

Terminology and information on torpedinoid anatomy including chondrocranial and hyobranchial morphology follows Henle (1834), Gill (1862), Haswell (1895), Garman (1913), Holmgren (1941), and Compagno (1973, 1977, 1988, 1999a). Clasper terminology for torpedinoids follows Leigh-Sharpe (1922, 1924, 1926) and Compagno (1988).

ORDER RAJIFORMES, SUBORDER TORPEDINOIDEI - ELECTRIC RAYS

DEFINITION (derived from Compagno (1973, 1977, 1999a). Rays (Rajiformes) with head broadly depressed and included with body and hypertrophied pectoral fins to form a thick, flattened, oval, circular or subquarate fleshy pectoral disc with broadly rounded apical margins. Trunk thick, broad, and depressed, not rising abruptly dorsal to pectoral bases. A pair of large, kidney-shaped electric organs in disc between propterygium, branchial region and pectoral girdle, generally visible through skin of ventral surface. Precaudal tail usually stout and muscular, more or less elongated, but diminutive in Hypnidae; tail with two, one or no dorsal fins, ventro-lateral folds (often present) but no median dorsal or ventral skin folds; tail without caudal electric organs or a sting. Preoral snout short to moderately long, 6-21% of total Total length, broadly rounded or truncated, front edge continuous with that of the pectoral disc and not angular, not formed into a tooth-studded rostral saw. Eyes small to moderate-sized in most taxa (eyes vestigial in some *Narke dipterygia* and absent externally in *Typhlonarke*) dorsal on the head, well medial to lateral margins of disc and anterior to spiracles; eyes with a velum on the cornea but no semilunar groove below them. Spiracles either contiguous with rear margins of eyes or separated from them by a space less than their width; spiracles with internal pseudobranchs. Nostrils moderately large, close together, just anterior to mouth; circum-narial flaps and grooves well developed on incurrent apertures of nostrils; anterior nasal flaps fused medially to form a broad nasal curtain, which is free posteriorly and usually reaches mouth; broad nasoral grooves present between excurrent apertures of nostrils and mouth. Mouth always subterminal on head although varying in position (close behind front edge of snout in *Electrolux*), small to moderate-sized, straight or arcuate. No gill sieves or rakers on internal gill slits. Teeth small and not fused into crushing plates; dental bands limited to medial half of jaws, not extending to mouth corners; teeth in 8-68 / 7-75 rows, total rows 15-141; tooth crowns carinate, monocuspidate or tricuspidate. Skin completely naked on all surfaces of disc, tail, fins, and claspers. Pectoral fins expanded, fused medially with head and trunk, usually not obviously distinct externally; pectoral fin bases very long, extending from nasal capsules to pelvic fin origins; pectoral axils much closer to vent than to first gill apertures. Propterygia of pectoral fin skeleton greatly elongated, longer than metapterygia, segmented anteriorly and forming a propterygial axis; propterygia reaching level of nasal capsules or ending behind them, radials extending in front of nostrils but not reaching snout tip. Mesopterygia large and expanded anterolaterally to opposite posterior quarter to half of basal segment of propterygial axis, and

carrying its radials. Scapulocoracoids with a pair of lateral bars connecting coracoid bar with scapular processes on each side, separated by a large fenestra from lateral face of scapulocoracoid, which forms unique hollow tube, more or less elongated posterolaterally and terminating in a small, rounded-oval articular surface with a distinct procondyle for the propterygium, small anterodorsal and anteroventral foramina above and below a broad anterior bridge between the procondyle and a small mesocondyle for the mesopterygium, small postdorsal and postventral foramina, and a moderate-sized metacondyle for the metapterygium. Suprascapulae fused together above synarcual or behind it and above neural spines of free monospondylous vertebrae; suprascapulae without the complex attachment to vertebral column as in other batoids; distal ends of suprascapulae straight and not forked, articulating with scapular processes. Pelvic fins not divided into distinct anterior and posterior lobes (except in *Typhlonarke*, where the anterior lobes are fused with and protrude from the pectoral disc and the posterior lobes are fused to the posterior disc). Origins of pelvic fins anterior to pectoral free rear tips; pelvic fins with straight, convex, or concave posterior margins. Pelvic girdle with strong lateral prepelvic processes, short ischial and iliac processes, but without a medial prepubic process on puboischiadic bar; puboischiadic bar posteriorly arched or transverse, not anteriorly arched. Claspers short, stout, and protruding a short distance past pelvic free rear tips or not at all in adult males; clasper glans very simple, with small pseudosiphon and pseudopera but without clasper spines. Dorsal fins usually two (one in *Narke* and *Typhlonarke*, absent in *Temera*), moderately large (small in Hypnidae) and rounded-angular (not falcate). First dorsal fin when present with base over or just behind pelvic bases and over anterior half of precaudal tail. Caudal fin usually large to moderate-sized (small in Hypnidae); caudal fin vertebral axis horizontal to weakly diagonal and elevated, diphycercal or weakly heterocercal; dorsal and ventral caudal fin margins broadly rounded, terminal lobe mostly rounded or occasionally pointed, a low ventral caudal lobe present or absent; caudal fin without a differentiated postventral margin and without a discrete terminal lobe and subterminal notch. Vertebral column with cervicothoracic synarcual but no thoracolumbar synarcual; synarcual variable in length, ending before or behind suprascapulae; synarcual not formed anteriorly into a collar-like sheath around spinal cord but with a peg-like ventral projection fitting in foramen magnum and between occipital condyles. Cranium with rostrum variably developed, absent (Hypnidae), more or less reduced (Torpedinidae, Narkidae) or moderately large, wide, and trough-shaped (Narcinidae). Precerebral cavity more or less expanded into rostrum but not roofed dorsally, truncated anteriorly in Narkidae. Rostral nerves not enclosed in rostrum. Nasal capsules expanded laterally, ventrolaterally, ventrally or anteroventrally; internasal septum broad and depressed (Narcinidae) to more or less narrow and compressed (Hypnidae, Narkidae), broadly separating the nasal capsules or not. Antorbital condyles on anterior, lateral or posterior surfaces of nasal capsules; antorbital cartilages distally expanded, directed anteriorly or anterolaterally, fan-shaped or antler-shaped and branched; antorbital cartilages not articulating with propterygia. Preorbital processes rudimentary or absent, no supraorbital crests, no postorbital processes and no low suborbital shelves. Anterior fontanelle not delimited anteriorly by a transverse ridge. Cranial roof with frontoparietal fenestra absent or very small to huge; separated from anterior fontanelle by an epiphysial bar or not. Basal plate flat or arched and without basal angle; basal plate with a single internal carotid foramen or two narrowly separated carotid foramina at its midline. Occipital condyles small, ventral, and not covering occiput. Dorsal and ventral labial cartilages present in Narcinidae and Narkidae; absent and presumably lost in *Hypnos* and *Torpedo*. Hyobranchial skeleton without basihyoid element; hypobranchials discrete, parasagittal, not fused to form a midventral plate and not fused to well-developed basibranchial copula. Branchial rays expanded distally as broad circular plates. Mode of reproduction ovoviviparous as far as is known, with prenatal young nourished primarily by their yolk sacs.

ELECTROLUX COMPAGNO & HEEMSTRA, *genus novum.*

TYPE SPECIES: *Electrolux addisoni* Compagno & Heemstra *sp nov.* described below.

GENERIC DIAGNOSIS: Narkid electric rays with subcircular disc, length 51% TL; snout short, broadly rounded and nearly straight (Figs 1- 4). Eyes well-developed, close to front edge of disc, but mostly hidden by loose skin. Spiracles (Fig. 5) contiguous with eyeballs, rim a low, rounded, ridge with 5 or 6 long, slender stiff papillae and 2 or 3 short, soft papillae, including one minute papilla on eye; spiracle diameter ~ 1.1-1.3 times eye diameter. Incurrent apertures of nostrils nearly circular, flaps of incurrent apertures (circumnarial flaps) broad, large, flattened, trumpet-like and elongated, their length 2/3-3/4 length of anterior nasal flaps; posterior margin of nasal curtain deeply incised, with prominent lateral lobes and a small medial lobe; ventral surface of curtain with a shallow medial groove; length of anterior nasal flap about 1.1 in outer internarial width; lateral margins of curtain nearly parallel. Mouth and nostrils projecting ventrally from disc as a prominent nasoral turret (Figs 6A & 7) near front edge of disc. Lips between labial folds and dental bands thin and with small transverse pleats of skin; lower lip narrow and thin, no mental

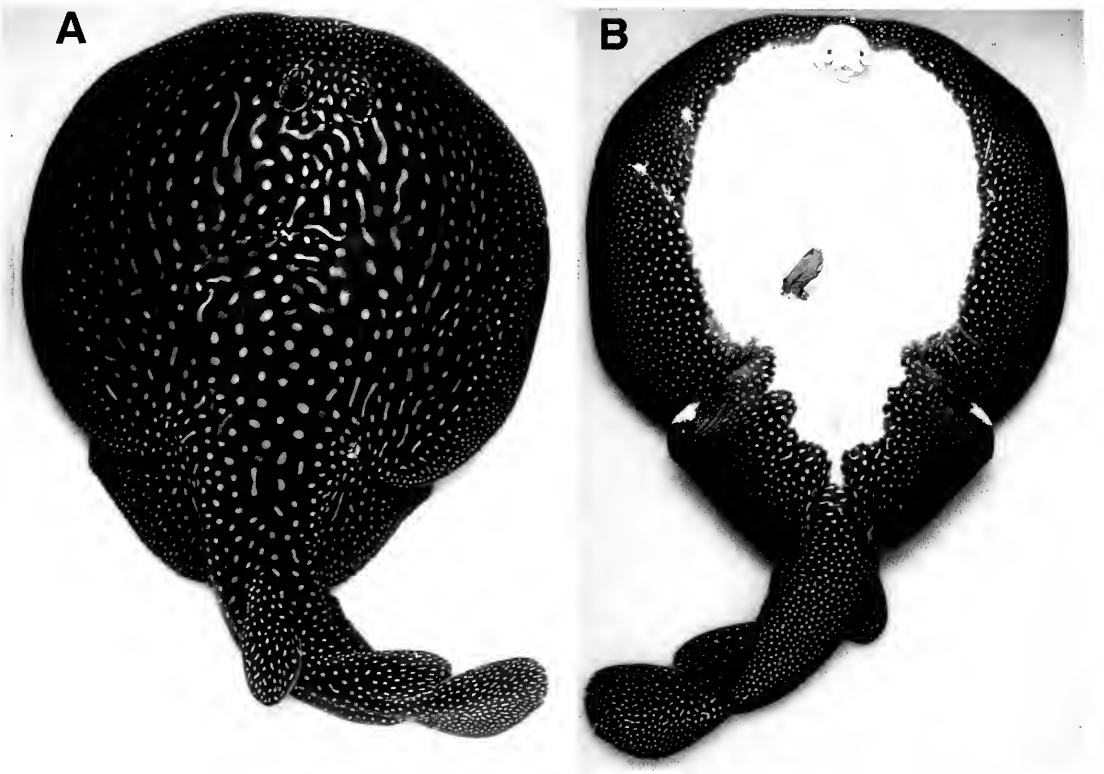

Figure 3. Holotype of *Electrolux addisoni*, 515 mm TL adult male, in A, dorsal and B, ventral views. Note differences in dorsal disc colour pattern compared with live animals (Figs. 1 & 2).

Figure 4. Paratype of *Electrolux addisoni*, 502 mm TL, adult male, in A, dorsal and B, ventral views.

Figure 5. Photos of left eye and spiracle (anterior to left) of: A. *Electrolux addisoni*, holotype, with papillose depressed spiracular rim. Pin penetrates skin at base of ocular papilla, forceps are clamped on fleshy lower eyelid. B. *Heteronarce garmani*, SAM 34813, 289 mm TL adult male, with smooth elevated spiracular rim. Photographs by authors. Scale bars = 5 mm

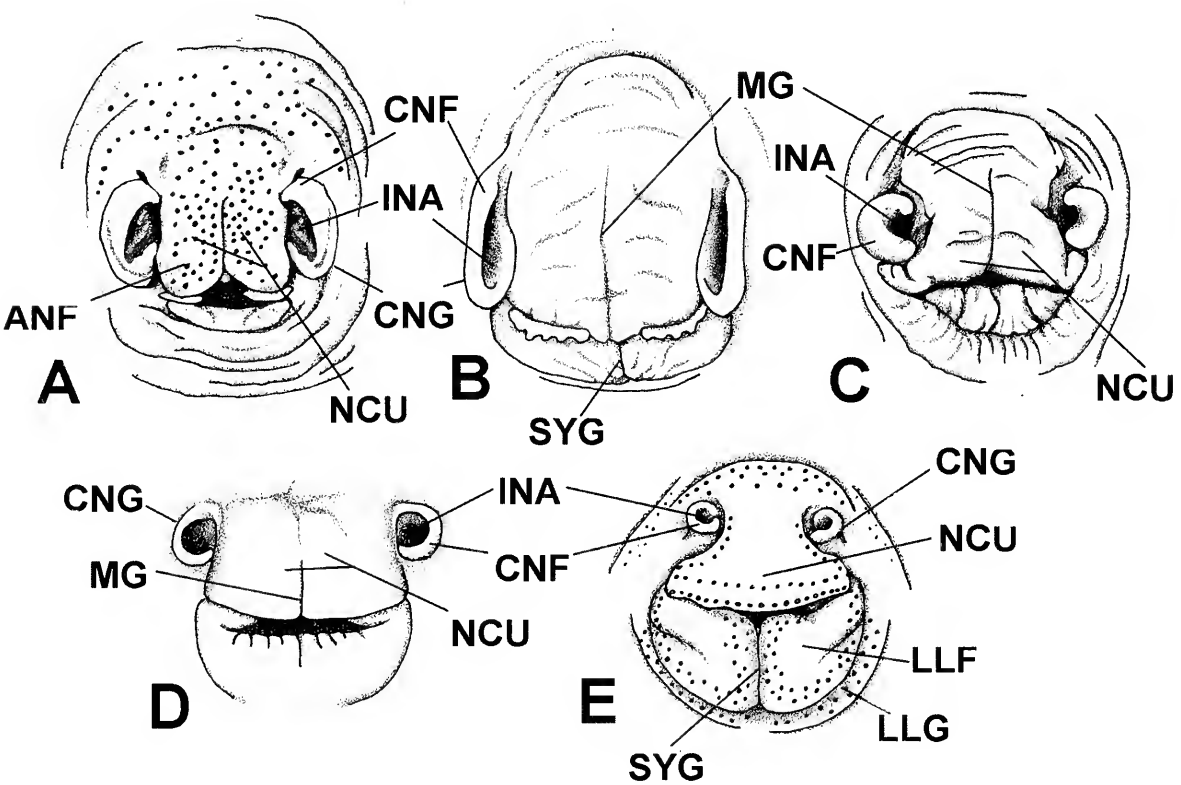

Figure 6. Mouth and nostril drawings of A. *Electrolux addisoni,* holotype. B. *Heteronarce garmani*, RV *Benguela* G13531 88N 30-08, 125 mm TL female. C. *Narke capensis*, SAM uncataloged, 265 mm TL adult male. D. *Temera hardwickii*, SU-35728, 104 mm TL adolescent male. E. *Typhlonarke aysoni* from SIO 61-149-6A and Garrick (1951). Drawings by Elaine Heemstra based on specimens and sketches or photographs by LJVC . Abbreviations: ANF, anterior nasal flap; CNF, circumnarial fold; CNG, circumnarial groove; INA, incurrent aperture; LLF, lower labial fold; LLG, lower labial groove; MG, medial groove on nasal curtain; NCU, nasal curtain; SYG, symphysial groove.

groove, but ventral dental band bisecting it medially; lower labial folds and grooves short, ending far lateral to midline of mouth (Figure 7); labial cartilages very small, their bases well lateral to symphyses. Total tooth row counts 32-34 or 15-16 / 17-18. Superscapulae C-shaped (Fig. 13A), situated anterior to coracoid bar. Total pectoral radials 47-53; metapterygial axis not greatly reduced in length, with equal numbers of radials to propterygium (17-19 each); no neopterygial radials on scapulocoracoid. Pelvic fins not divided into discrete anterior and posterior lobes. Puboischiadic bar with stout angular iliac processes (Fig. 14A). Total basipterygial pelvic radials 17-19, Claspers short and extremely flat in adult males (Figure 15), not extending past pelvic free rear tips. Two dorsal fins, subequal in area, second dorsal slightly smaller than first, first dorsal origin over pelvic free rear tips and well behind pelvic insertions. Lateral tail folds broad. Total synarcual segments 14-16, monospondylous precaudal centra 30, diplospondylous precaudal centra, 61- 62, precaudal centra 96-97, precaudal total segments 105-108, total free centra 118-120, total centra 123-125, total segments 132-136. Neurocranium with a narrow, large, erect, flattened medial rostral cartilage, and two lateral rostral cartilages below it forming a large ventrally-directed yoke-like structure (Fig. 9); antorbital cartilages with narrow anterior branched ends (Figs 11 and 12); ethmoid region of chondrocranium laterally compressed, strongly bent and expanded ventrally; no frontoparietal fenestra; otic capsules small and not expanded laterally. Jaws antero-ventro-medially expanded, palatine processes of palatoquadrates nearly straight. Second hyobranchial cartilages large, Intestinal valve count 17 (paratype). Mature males 50-52 cm. TL. Elaborate colour pattern of pale spots on dark brown background present on most of body; dorsal surface of disc of living rays with concentric black lines and pale spots.

Derivation of generic name: The name alludes to the well-developed electrogenic properties of this ray (collectors and photographers have experienced the shocking personality of this bold, active and brightly patterned electric ray first-hand), the discovery of which sheds light (Latin, *lux*) on the rich and poorly-known fish diversity of the Western Indian Ocean. And the vigorous sucking action displayed on the videotape of the feeding ray that was taken by Stephania and Peter Lamberti may rival a well-known electrical device used to suck the detritus from carpets, furniture, and other dust-gathering surfaces in modern homes. The gender of the name *Electrolux* is feminine.

Comparison with other genera: *Electrolux* differs from all other narkids including *Heteronarce* in having large spiracular papillae (Fig. 5); very broad, elongated and flattened circumnarial flaps (Figure 6; flaps narrower and usually shorter in other narkids); prominent anterior nasoral turret; narrow thin lower lips without a mental groove (lower lips large and with a mental groove in other genera); small labial cartilages and labial folds ending well lateral to midline of mouth (Fig. 7) labial folds enlarged and meeting at midline of mouth in other genera); broad lateral tail folds (tail folds narrow in other narkids and obsolete in *Typhlonarke*); pectoral radials more numerous (47-53 versus 40-43 radials in other narkids); metapterygia not reduced and radials equal to propterygial radials (metapterygia shorter and their radials fewer than propterygial radials in other genera); claspers not extending past pelvic fin free rear tips (extending past pelvic fin tips in most narkids except *Typhlonarke aysoni* and some *Narke capensis*); higher vertebral counts for most vertebral count groups (Table 6); chondrocranium with enlarged medial rostral cartilage and enlarged yoke-shaped lateral rostral cartilages (Fig. 9); rostral cartilages small and slender in other genera (as in Fig. 10); compressed, ventrally bent and expanded ethmoid region (laterally expanded in other taxa); antorbital cartilages with very narrow branched anterior section (broadly branched in most narkids); palatine processes of palatoquadrates straight, not curved medially; higher intestinal valve counts (17 in *Electrolux* vs. 8-10 in other genera); greater size (see discussion below); and unique coloration.

Electrolux and *Heteronarce* are the only narkid genera with two dorsal fins. Two dorsals are primitive for torpedinoids and for batoids, but *Narke* and *Typhlonarke* have one dorsal fin in the position of the first dorsal fin of *Electrolux* and *Heteronarce* and presumably have lost their second dorsal fins, while *Temera* has no dorsal fins. *Electrolux* and *Heteronarce* also agree in their nearly parallel-edged anterior nasal flaps (nasal flaps more divergent in other narkids, particularly *Typhlonarke* and *Narke*), long and thinner circumnarial flaps (short and thick in other narkids), larger rounded-angular basibranchial copula (copula reduced and tack-shaped in *Narke* and *Temera*), and the lack of a frontoparietal fenestra (*Narke, Temera*, and *Typhlonarke* with prominent fenestra). nostrils with circular rather than elongate-oval incurrent apertures; a V - shaped posterior margin on its nasal curtain (nearly straight in *Heteronarce*); short, stout iliac processes on the pelvic girdle (Fig. 14A, iliac processes slender, long, curved and attenuated at least in *H. bentuvai, H. garmani* and *H. mollis*); and more tooth rows (Table 4; total 32-34 vs 20-24 in *Heteronarce*).

Electrolux additionally differs from *Typhlonarke* in having well-developed eyes (rudimentary in the latter genus and absent externally), a medial groove on its nasal curtain (absent in *Typhlonarke*), a trilobate V-shaped posterior edge on its nasal curtain (transverse and undivided in *Typhlonarke*), more tooth rows and smaller teeth (32-34, vs. 15-24 total in *Typhlonarke*), a stouter precaudal tail, undivided pelvic fins without leg-like anterior lobes, and longer more slender jaws (jaws short and very stout in *Typhlonarke*). *Electrolux* differs from *Narke* in having shorter iliac processes on its pelvic girdle.

Species: A single known species, *Electrolux addisoni* Compagno & Heemstra, described below.

***Electrolux addisoni* sp. nov.**
Ornate sleeper-ray
Figures 1-4, 5A, 6A, 7A, 8, 9A, 11A, 12A, 13A, 14A, 15, 16A, 17A, 18.

Heteronarce? sp. nov. Compagno, 1999b: 116.
Undescribed genus and species. Compagno, 2005: 529.

Holotype: SAIAB 78777, adult male, 515 mm TL, 305 mm disc width, Indian Ocean on reef off Manaba Beach near Margate, southern KwaZulu-Natal, 30°51.4′ S, 30°23.1′ E; depth 6-12 m; collected by Mark Addison, September 2003.

Paratype: SAM 36908, adult male, 502 mm TL, 291 mm DW, locality the same as in holotype but collected by Brent Addison, October 2003.

DESCRIPTION. Measurements in millimetres and proportions as percentages of total length (TL) are presented in Table 2 for the types of *Electrolux addisoni*. Disc subcircular, thick and fleshy; greatest width slightly more (1.1-1.2 times) than its length. Edge of disc a continuous curve, anterior edge nearly straight but broadly curving to sides of disc, with snout, pectoral anterior margins, pectoral apices, and the posterior and inner pectoral margins not distinct but continuously curving rearwards, mesially, and recurving anteriorly to form broad but discrete free rear tips before merging with the sides of tail base. Snout short, preorbital length 6.4-8.2 % TL, preoral length 6.2-8.4 % TL. Prespiracular head length 2.4-2.7 times interspiracular width, preoral length about 1.8-2.6 times as great as outer internarial width. A pair of small endolymphatic foramina on nuchal region of head about eye-length behind spiracles and about on anterior-posterior line tangent to their inner margins. Electric C- or narrowly kidney-shaped and about three times as long as wide; organs not obvious through skin of dorsal surface but prominent on white medial area of ventral surface; electric organ cells rounded-oval to hexagonal, count of cells for right organ approximately 289 on paratype. Vent anterior to pelvic inner margins and free from them, vent long and with broad lateral folds and conspicuous abdominal pores on the folds of the posterior third of vent. Tail stout, depressed, horizontally oval in cross section, with cutaneous lateral folds (about 7 mm wide) along lower part of tail from above rear end of pelvic fins and below midbase of first dorsal fin to base of caudal fin; tail moderately flattened below folds but broadly convex above; tail from vent to caudal tip about 1.3 times as long as snout-vent length; caudal peduncle nearly flat below folds, narrowly convex above them. Interdorsal space 75-106 % of first dorsal fin base; dorsal-caudal space 70 to 71 % of second dorsal fin base.

Eyes well-developed, protruding above surface of disc, posterior to a transverse vertical plane at mouth; upper eyelids thickened, lower eyelids enlarged and apparently mobile, capable of covering palpebral apertures. Eyeball included in anterior edge of spiracle; dorsal rim of spiracle with 8 slender papillae (Fig. 5), their configurations symmetrical between right and left spiracles and arranged as follows: measurements of left spiracle papillae of holotype, followed by lengths of paratype's papillae in parentheses, first (anterior-most) papilla short, soft, recumbent on top of fleshy orbit, 2.5 mm (2.8 mm); second and third papillae (proceeding clockwise around spiracle rim) cuneate, flattened and stiff, lengths 4.4 (4.5) and 4.7 (3.8) mm respectively; fourth papilla stiff, flattened, resembling a forefinger and short thumb, lengths 6.1 (6.1) and 1.6 (2.0) mm respectively; fifth papilla short, simple, sausage-shaped, 2.6 (1.7) mm; sixth, seventh and eighth papillae long, slender, stiff, and finger-like, lengths 4.8 (4.1), 4.2 (3.5) and 8.0 (4.8) mm respectively. The spiracle papillae are bilaterally symmetrical for the left and right spiracles, with the three long, slender papillae on the lateral margins, short fleshy papilla on top of eyes, finger and thumb papilla on posterior rims and two cuneate papillae on medial edges of spiracles.

Nostrils undivided, incurrent apertures with trough- or trumpet-shaped circum-narial folds (Fig. 6A), resembling a funnel cut in half vertically and separate from mouth; circumnarial folds somewhat expanded ventrally. Nasal curtain fleshy, elongated, with numerous small pores and a median longitudinal groove or sulcus on its ventral surface; distal (posterior) edge of curtain emarginate and trilobate, with a short, bifid fleshy barbel-like anterior nasal flap at each lateral corner with broadly rounded posterior ends, and a short barbel-like lobe on midline of inner surface ; with mouth closed, the nasal curtain extends over front of lower jaw. Each anterior nasal flap has a strong mesonarial flap above (dorsal to) its posterior tip. Excurrent apertures moderately large, hidden ventrally by nasal curtain and circumnarial folds but open broadly above them to posterior surface of snout in front of mouth, internarial space between inner ends of excurrent apertures hidden, internarial space about 3.7-4.0 in mouth width when jaws are retracted and mouth closed.

Gill openings small, width of fifth 0.4-0.8 times width of first gill opening and 1.9-2.8 in spiracular length; distance between inner ends of first pair of gill openings about 2.9-3.0 times interspiracular width and about 1.5-1.9 times distance between fifth pair.

Mouth protrusile but scarcely distensible; mouth and jaw tips apparently forming a short tube when protracted and opened; lips thin, transversely-pleated, projecting (Fig. 7A) and surrounded by a shallow groove; lips pleated between lateral edges of dental bands and small labial folds; no prominent groove between labial folds, which include labial cartilages at

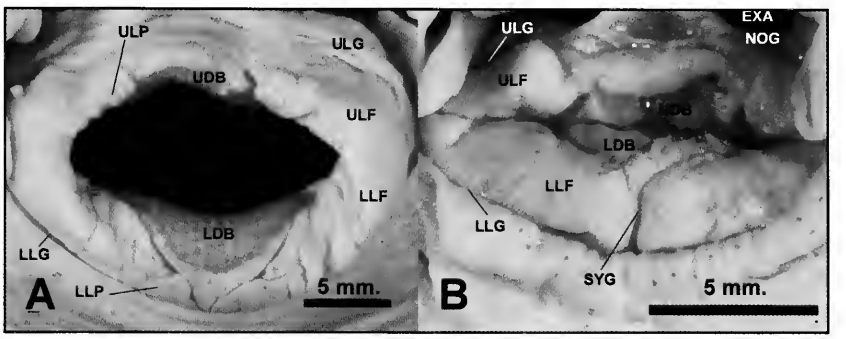

Figure 7. Mouth with nasal curtain lifted of A. *Electrolux addisoni*, paratype, mouth opened. B. *Heteronarce garmani*, SAM 34813, 256 mm TL adult male, mouth closed, upper dental band partly obscured by debrisScale bars = 5 mm Abbreviations: EXA, excurrent aperture; LDB, lower dental band; LLF, lower labial fold; LLG, lower labial groove; LLP, lower labial pleats; NOG, nasoral groove; SYG, symphysial groove; UDB, upper dental band; ULG, upper labial groove; ULF, upper labial fold; ULP, upper labial pleats.

corners of mouth; mouth width 3.7-4.0 times in interspiracular distance and 1.5-1.6 times spiracle length.

Tooth bands occupy about half of mouth width, firmly connected to jaw cartilages by connective tissue, band widths greater than inner internarial distance. Teeth in quincunx arrangement, forming a tessellated pavement. Tooth formula 7-8~1~7 / 8~1~8-9, tooth row counts 15-16 / 17-18 rows or 32-34 total rows; ca. 6 - 8 series functional, as indicated by wear on crowns. Teeth very small, similar in both jaws and similar from symphysis to mouth corners, teeth in midline of mouth about 1 mm wide across crown foot and lateral teeth slightly smaller; labial surface of crown obliquely flattened, extending lingually as a single small stout cusp (Fig. 8) worn-off on most functional teeth); prominent basal ledge and groove on crown; roots small and lingually projecting, divided ventrally by a transverse groove; no teeth exposed on ventral surfaces of jaws when mouth is closed, but dental bands visible along anterior edge of jaws.

Pectoral girdle crescentic in dorso-ventral view (Fig 13A). Anterior margin of coracoid cartilage concave medially but convex laterally. Propterygium a narrow segmented axis, articulates with procondyle of lateral face of scapulocoracoid, curves anteriorly, and is divided into 6 axial segments, the distal-most segment poorly calcified; mesopterygium elongated and unsegmented, articulating with the mesocondyle on lateral scapulocoracoid face and runs parallel to proximal segment of propterygium; metapterygium forming an axis of 4 segments, the proximal segment articulates with metacondyle on posterior corner of lateral face of scapulocoracoid and the distal segments extend rearwards into the pectoral base and free rear tip. 17 or 20 pectoral radials on propterygium, 12 or 13 on mesopterygium and 17 or 20 on metapterygium, total radials 46 or 53; no neopterygial radials articulating on lateral face of scapulo-coracoid; distal 2-4 segments of pectoral radials are bifid.

Pelvic fins separate, deltoid-rounded anterior corner rounded, posterior (lateral) edge slightly convex, fairly thick and fleshy, pelvic fin origins well anterior to pectoral fin insertions; anterior edge stiff and thick, supported by the densely calcified anterior radial, apices broadly rounded, posterior (lateral) edge nearly straight or slightly convex when fins are fully spread; free rear tips well-developed, narrow, rounded-subangular, inner margin of pelvics distinct, not attached to sides of tail at free rear tips; no frenum between pelvic inner margins; pelvic fin length ~ 40-43 % disc width. In live animals the pelvics are often broadly spread and appear rounded rather than angular. Pelvic girdle (puboischiadic bar) broad (Fig. 14A), its median antero-posterior width equals one sixth of girdle's transverse length; prepelvic process at each lateral end of girdle thin and weakly calcified extending anteriorly for the lengths of 7 centra. Iliac

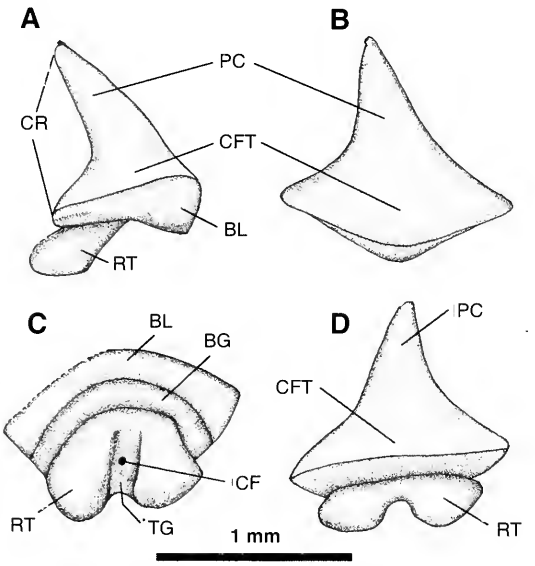

Figure 8. Lower replacement tooth (cusp unworn) from symphysis, removed from lingual end of dental band in the paratype of *Electrolux addisoni*, A. Lateral view. B. Labial view. C. Basal view. D. Lingual view. Abbreviations: BG, basal groove; BL, basal ledge; CF, central foramen; CFT, crown foot; CR, crown; PC, primary cusp; RT, root; TG, transverse groove.

processes well-developed on pelvic girdle, expanded dorsally from lateral node, these short, stout, nearly straight, and angular; large basal condyle present on postero-lateral surface of each lateral node for articulation of long pelvic basipterygium, a short but prominent, blunt ischial process present on lateral node medio-posteriorly to basal condyle and mesial to basipterygium. 17 or 19 radials articulating with pelvic basipterygium, plus anterior enlarged radial (apparently a fused double radial) articulating with lateral node of pelvic girdle; the enlarged anterior radial projects postero-laterally and supports the leading edge of the pelvic fin.

Claspers broad, flat and short (Fig. 15), nearly reaching free rear tips of pelvics ; clasper depth at base about 2.7 in base width and with a depressed elliptical cross-section; in dorso-ventral view claspers with parallel sides and a broad, bluntly rounded tip; in lateral view, dorsal and ventral surfaces nearly parallel along their lengths but with a short tapering posterior tip. Dorsal clasper groove open, with apopyle dorsolateral on base of clasper and hypopyle dorsal on glans; clasper glans with a long, low flap or cover rhipidion on the mesial edge of groove, a long slit-like pseudosiphon (*slot* of Leigh-Sharpe, 1922) mesial to cover rhipidion and near rear tip of clasper, and a long pseudopera (*slit* of Leigh-Sharpe, 1922) on postero-lateral tip of clasper.

Dorsal and caudal fins compressed, flexible and close together; first dorsal fin origin above axil between inner edge of pelvic fin and clasper, or about opposite pelvic insertions; apex of first dorsal fin reaches past level of second dorsal fin origin; apex of second dorsal fin reaches well past caudal fin origin; dorsal fins similar in shape, but first dorsal fin slightly larger than second, second dorsal fin height 81- 86 % of first dorsal height, and second dorsal base 86-97 % of first dorsal base; anterior margin of dorsal fins strongly sloping and broadly convex, apices broadly rounded; posterior and inner margins weakly differentiated and convex; first dorsal base about 41-47 % of anterior margin; second dorsal fin base about 41% of anterior margin. First dorsal fin with 6 radials, second dorsal fin with 7; dorsal-fin radials divided into 3 or 4 segments.

Caudal fin fairly high, short, and oval, its lower rear edge forming a continuous broad convex curve to tip of fin, upper margin slightly less convex, tip broadly rounded; vertebral column axis slightly raised; hypaxial lobe narrower than epaxial lobe; fin height 70-78 % of dorsal caudal margin, which is 1.5-1.6 times in distance from first dorsal origin to upper caudal origin. Caudal fin with 25 dorsal radials (radials 21 & 22 fused at the base) and 31 ventral radials, plus a V-shaped terminal radial.

Antorbital cartilages short, directed anteriorly, with expanded posterior condyle for articulating with sockets on nasal capsules, with narrow shaft and moderately expanded, weakly branched anterior end, separated from anterior extensions of proterygia by ~ 4 cm; rear surface of chondrocranium with two prominent occipital condyles fitting two lateral sockets on anterior surface of synarcual.

Hyomandibula large (Figs 11A & 12A), articulating directly to lateral edge of lower jaw (Meckel's cartilage). On radiographs (Fig. 12A; also in *Heteronarce*, Fig. 12B), the synarcual seemed to be divided into anterior and posterior segments above the fourth gill arch, but detailed investigation of radiographs and dissection of the paratype revealed that the 'joint' between the two sections was the superimposed anterior edge of the basibranchial copula; a lateral strut on each side that seems to extend from the synarcual to the scapulocoracoid is the fifth ceratobranchial, which extends from the basibranchial to the scapulocoracoid. Vertebral counts are listed in Table 6. Spiral intestinal valve with 17 turns in the paratype (Table 7).

Live colour: The spectacular and elaborate dorsal colour pattern of live *Electrolux addisoni* is shown in Figures 1 and 2. The dorsal surface and most of the ventral surface of the disc and pelvic fins, the claspers, the tail and median fins are dark brown covered with dense small pale spots which are white in the preserved types (Figs 3 and 4) but pale yellow in life. The pale spots are larger on middle of dorsal disc, where there are several scattered, short, pale streaks; also light streaks irregularly present in dark ventrolateral surfaces of disc and anteroventral surfaces of pelvic fins near apices. In life the ray is covered with mucus, and there are several curved,

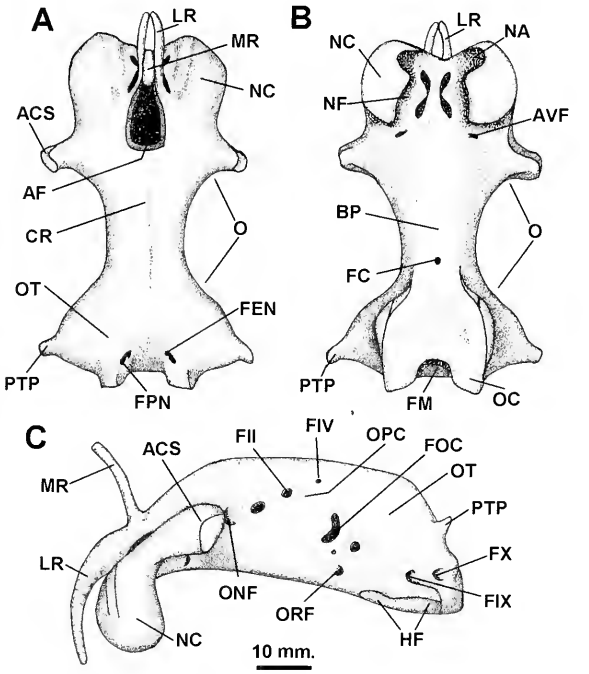

Figure 9. Chondrocranium of *Electrolux addisoni*, paratype, in **A.** dorsal, **B.** ventral, **C.** lateral views. Abbreviations: ACS, articular socket for antorbital cartilage; AF, anterior fontanelle; AVF, foramen for orbitonasal vein draining nasal sinus; BP, basal plate; CR, cranial roof; FII, fenestra for optic nerve; FIV, foramen for trochlear nerve; FIX, foramen for glossopharyngial nerve; FX, foramen for vagus nerve; FC, carotid foramina; FEN, foramen for endolymphatic duct; FM, foramen magnum; FOC, fenestra for superficial ophthalmic nerve; FPF, frontoparietal fenestra; FPN, fenestra for perilymphatic space; HF, hyomandibular facet (double); LR, lateral rostral cartilage; MR, medial rostral cartilage; NA, nasal aperture; NC, nasal capsule; NF, nasal fenestra; O, orbit; OC, occipital condyle; ONF, orbitonarial foramina; OPC, socket for optic pedicel; ORF, orbital fissure; OT, otic capsule; PTP, pterotic process.

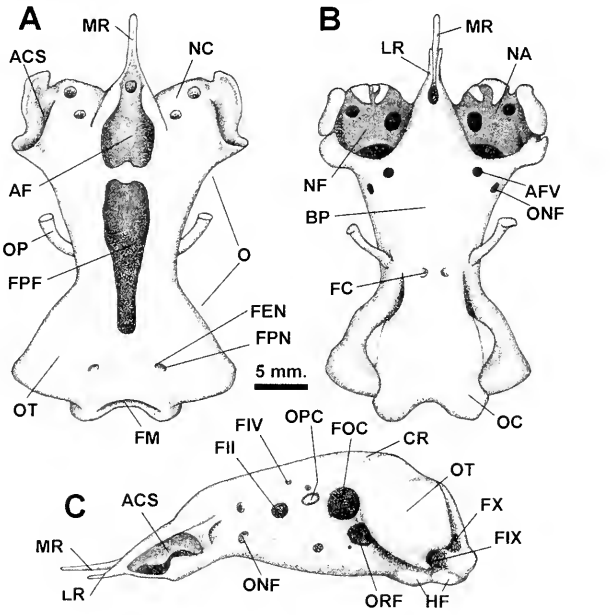

Figure 10. Chondrocranium of Narke capensis, Africana A12093 095 040 1035, 231 mm adult female, in A. dorsal, B. ventral, C. lateral views. Abbreviations as in Fig. 9.

(some concentric) black stripes on the dorsal disc which disappear when the mucus is rinsed off; the light spots and streaks are often obscured by sediment when the ray is at rest. Ventral surface of disc and pelvic bases abruptly white in center, forming a pear-shaped symmetrical blotch from the nasoral turret to the vent and pelvic insertions and including the gill slits and most of the electric organs (Figs 3B, 4B).

ETYMOLOGY. The species is named for Mark Addison, Managing Director of Blue Wilderness dive charters of Widenham, KwaZulu-Natal. Mr Addison collected the holotype and instigated the capture of the paratype. He has an extensive knowledge of the marine fish fauna of South Africa and has provided much valued assistance in our fish survey research.

SIZE: The holotype (515 mm TL adult male) weighed 1.8 kg., and the paratype (502 mm TL adult male) weighed 1.9 kg. *Electrolux addisoni* is apparently one of the largest members of the Narkidae, although females have yet to be examined, and the size range for maturation is unknown for males. Compagno & Last (1999a) noted that the Narkidae includes species that are adult at 9-46 cm TL and possibly reached a greater length, but *Electrolux* extends this to 52 cm, or possibly greater. Whitley (1940) stated that *Typhlonarke aysoni* reaches a far greater size than what is known for *E. addisoni*, with a maximum DW of about. 91 cm. and estimated TL over 122 cm. However, adult male specimens of *T. aysoni* examined by Whitley (1940), Garrick (1951) and by ourselves were only 21-38 cm. TL, and Garrick (1951: 5) repeated Whitley's comments but indicated that "most specimens taken are under 400 mm in total length". We wonder if Whitley's maximum DW figure (not his direct observation but based on the comment that "Graham records a maximum width of 36 inches") might be based on mistaken identity of the much larger *Torpedo fairchildi* for *T. aysoni*, although it is extremely difficult to mistake the two. The family Narkidae includes the smallest living batoids (Compagno *et al.*, 1999) and perhaps the smallest or at least the shortest, of the living chondrichthyans (Fig. 16). Males of *Temera hardwickii* examined by us are fully mature at 82-109

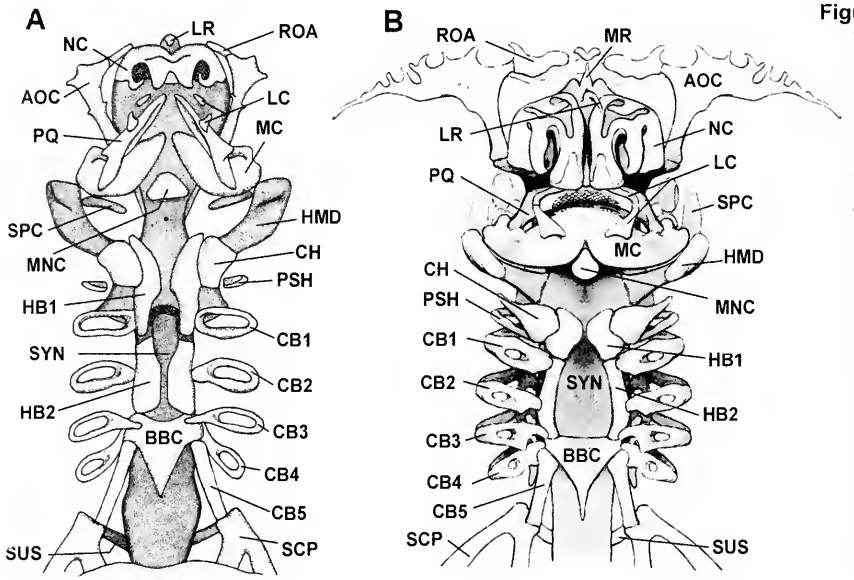

Figure 11. Narkid hyobranchial skeleton in ventral view. **A**. *Electrolux addisoni*, composite of SAIAB 78777 and SAM 36908, derived from radiograph of holotype and dissection of paratype. **B**, *Narke japonica*, drawing modified and simplified from Garman (1913: pl. 67, fig. 3) in ventral view. Abbreviations: AOC, antorbital cartilage; BBC, basibranchial copula; CB1-5, ceratobranchials 1-5; CH, ceratohyal; HB1-2, hyobranchials 1 and 2; HMD, hyomandibula; LC, labial cartilages: LR, lateral rostral cartilages; MC, Meckel's cartilage (lower jaw); MNC, mental or symphysial cartilage; MR, medial rostral cartilage; NC, nasal capsules; PQ, palatoquadrate (upper jaw); PSH, pseudohyoids; ROA, rostral appendix; SCP, scapular process of scapulocoracoid (shoulder girdle); SPC, spiracular cartilage; SUS, suprascapulae of scapulocoracoid; SYN, synarcual.

mm TL and females at 105-148 mm TL; the species has been reported as reaching 458 mm TL. Adult males of a dwarf species of *Narke* from the Taiwan Straits are 99-109 mm TL and possibly reach 149 mm (see study material). In comparison to these tiny narkids, *Electrolux addisoni* is a giant, with the holotype 6.3 times longer and 139 times heavier than the smallest adult male *T. hardwickii* examined by us (82 mm TL and 13 grams).

Available data for the smallest living sharks suggest that they may be almost twice as long as the smallest narkids. Compagno (1988: 24) discussed the minimum size of sharks and noted that although the diminutive dalatiid shark *Squaliolus laticaudus* is popularly considered the smallest living shark at a minimum adult length of 150 mm (Figure 16), it has several rivals of similar size. The proscylliid catshark *Eridacnis radcliffei* matures at 166-242 mm TL, with a 186 mm adult male weighing 14 gm, and a 242 mm pregnant female 37 gm. The etmopterid lantern shark *Etmopterus carteri* is adult at 186-212 mm, *E. perryi* is adult at 160-200 mm, *E. polli* is adult at 229-241 cm and probably smaller (a recently examined adult male is 195 mm long), and *E. virens* is adult at 181-257 mm. The dalatiid kitefin shark *Euprotomicrus bispinatus* is mature at 200-266 mm while the two *Squaliolus* spp. (*S. aliae* and *S. laticaudus*) are mature at 15 or 20-25 cm

BIOLOGICAL NOTES. *Electrolux addisoni* belongs to the sleeper ray family Narkidae, based on the genus *Narke* and Greek *narke*, numbness, torpor, that alludes to the sluggish nature of these sedentary rays and the numbing effects of their electric organs. *Electrolux addisoni* however, is far from torpid while feeding on the substrate (Fig. 2A), and vigorously thrusts its mouth into loose sand or gravel while walking actively on its spread pelvic fins. It may lie motionless on the substrate, but when approached can arch its back, curl its disc, and raise its tail to perform a possible threat-display directed at the photographer (Fig. 2B). The stomach contents of the paratype included the semi-digested and fragmentary remains of approximately eight polychaete worms (including a tube-worm) and at least one small shrimp-like crustacean. Stomach contents weighed 5.6 grams. *Electrolux* as an infauna or meiofauna feeder agrees with the South African narkids *Narke capensis*, which mostly eats polychaetes (Compagno *et al.* 1989), and *Heteronarce garmani* (one specimen examined, Benguela G13531 88N 30-08, 127 mm immature female), which had a stomach filled with mud-balls.

The conspicuous dorsal colour pattern of *Electrolux addisoni* combined with the ray's boldness and activeness near divers, and its possible threat display (Figure 2B) may be aposematic and indicates that the ray is well-armed with electric organs and should be avoided. On the shallow, well-lit reefs where *E. addisoni* has been found, its main potential predators may be large carcharhinoid sharks (requiem sharks, Carcharhinidae, and hammerheads, Sphyrnidae) and lamnoid sharks (ragged-tooth sharks and white sharks). Ebert (1990) found that two species of electric rays successfully defended themselves from much larger sixgill sharks (*Hexanchus*), which are apex predators with a broad prey spectrum. The small blind narcinid *Benthobatis yangi* from Taiwan was observed to repel a *Hexanchus nakamurai*. And two individuals of the larger torpedinid *Torpedo* cf. *nobiliana* from South Africa that were examined showed bite patterns of *Hexanchus griseus*, indicating that the sharks grabbed the rays but were repelled (probably with a shock) before they could inflict a strong and lethal bite. These

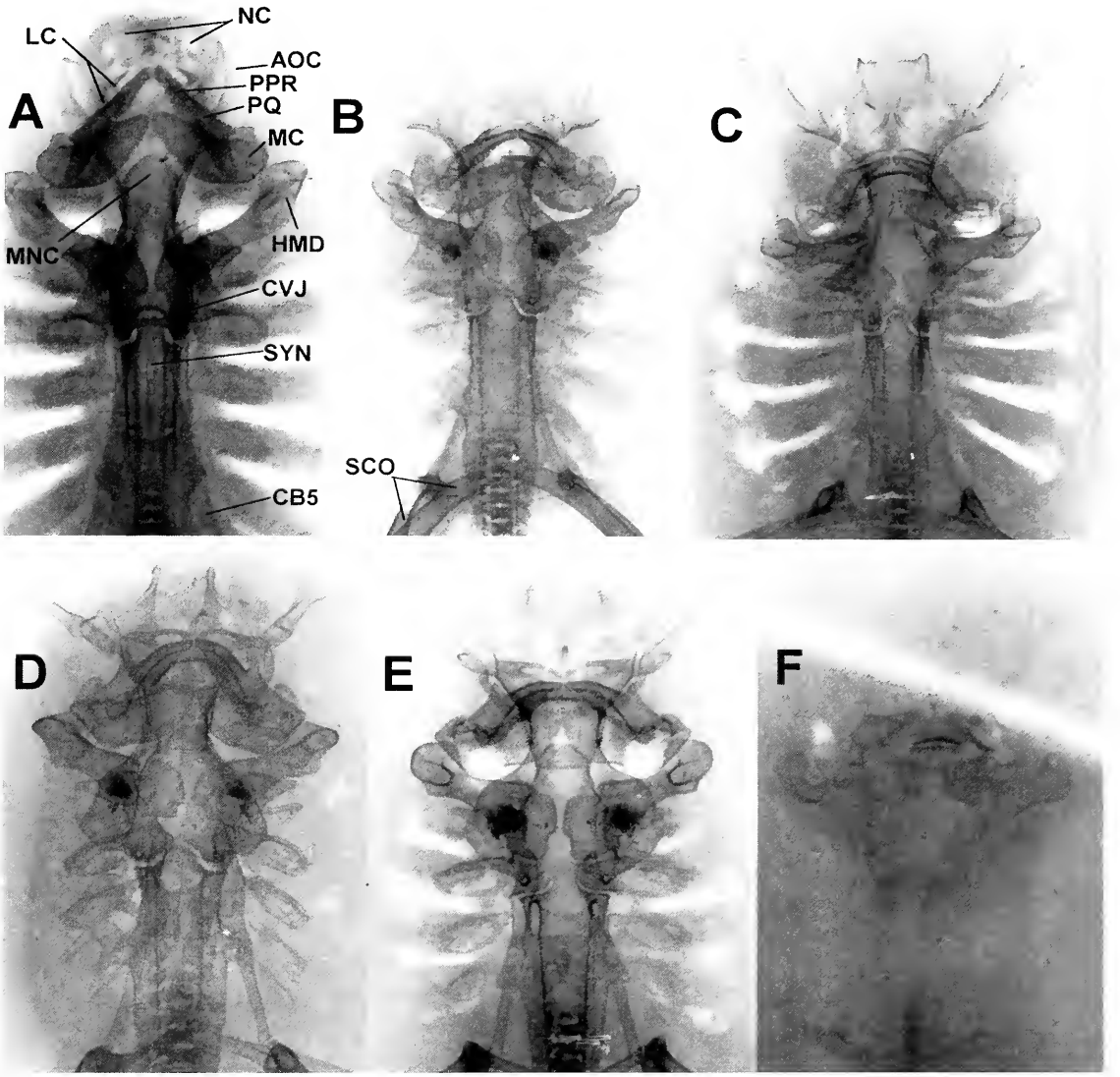

Figure 12. Narkid syncranium (neurocranium and splanchnocranium) and associated structures, monochrome inverted photographs from radiographs. A. *Electrolux addisoni*, holotype. B. *Heteronarce garmani*, **BMNH** 1921.3.1.3, 169 mm adult male holotype. C. *Heteronarce mollis*, **CAS** 58351, 218 mm TL female. D. *Narke dipterygia*, **SU**-41717, female ca. 135 mm TL. E. *Temera hardwickii*, **CAS** 58369, 108 mm TL female. F. *Typhlonarke aysoni*, **SIO** 61-149-6A, 92 mm TL immature female. Abbreviations: AOC, antorbital cartilage; CB5, 5th ceratobranchial (attaching basibranchial copula to scapulocoracoid; CVJ, occipito-cervical joint of chondrocranium and synarcual; HMD, hyomandibula; LC, labial cartilages; MC, Meckel's cartilage; MNC, mental (symphysial) cartilage; NC, nasal capsules; PPR, palatine process of palatoquadrate; PQ, palatoquadrate; SCO, scapulocoracoid (shoulder girdle); SYN, cervicothoracic synarcual.

incidents probably occurred in deep water where the sixgill sharks may have been using non-visual senses to locate their potential prey. Neither of these deep-water electric rays has a prominent colour pattern, and aposematic coloration and threat displays might be of little use to them in a visually limited environment. However, a quick defensive shock apparently can minimize damage by aborting a predator's attack. For the inshore *Electrolux addisoni*, aposematic coloration and a threat display might prevent a shark attack if the visual warnings are reinforced by a shock. There are other conspicuously marked inshore narcinids and torpedinids as well as the boldly marked narkid *Heteronarce bentuviai*, but their behaviour is for the most part poorly known.

Distribution and Habitat: As presently known, *Electrolux addisoni* is endemic to the east coast of South Africa in warm-temperate or subtropical waters along approximately 310 km of coastline with a very narrow continental shelf (10-36 km wide to the 200 m isobath) but the few sightings were all inside the 50 m isobath. It could be more wide-ranging elsewhere in warm waters of southern Africa and even off East Africa. Known localities (Fig. 17, map) are mostly from dive sites off south-central kwaZulu-Natal (depth and

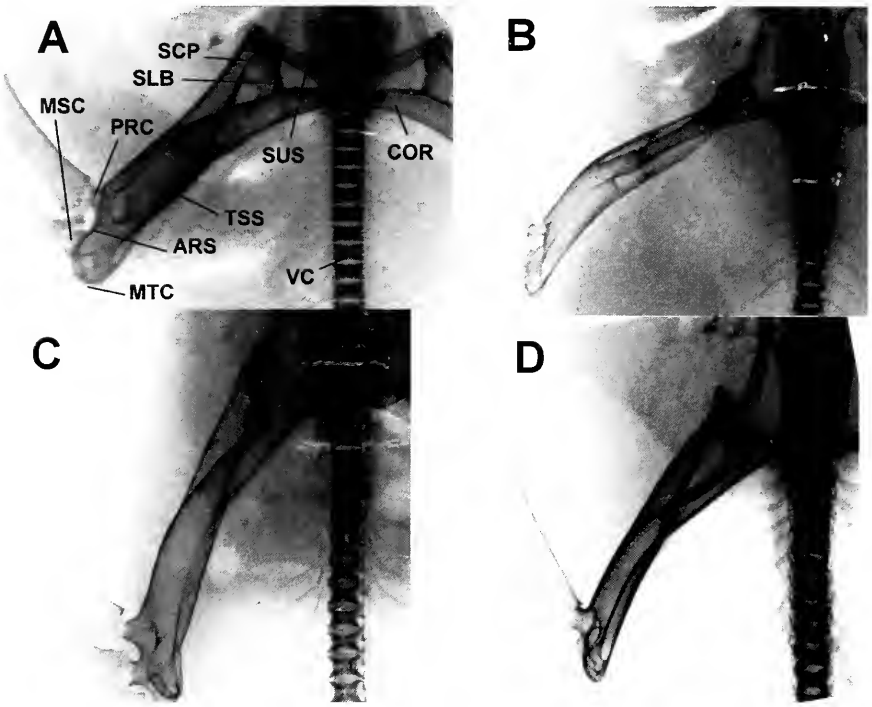

Figure 13. Narkid pectoral girdles (scapulocoracoids), radiographs showing left side in ventral view. **A**, *Electrolux addisoni*, holotype. **B**, *Heteronarce mollis*, CAS 58351, 218 mm TL female. **C**, *Narke japonica*, SU 61723, ca. 215 mm TL, female. **D**, *Temera hardwickii*, SU 35736, 105 mm TL, female. Abbreviations: ARS, articular surface; MSC, mesocondyle or mesopterygial condyle; MTC, metacondyle or metapterygial condyle; PRC, procondyle or propterygial condyle; SCP, scapular process; SLB, lateral bar; SUS, suprascapulae; TSS, tubular section; VC, vertebral column.

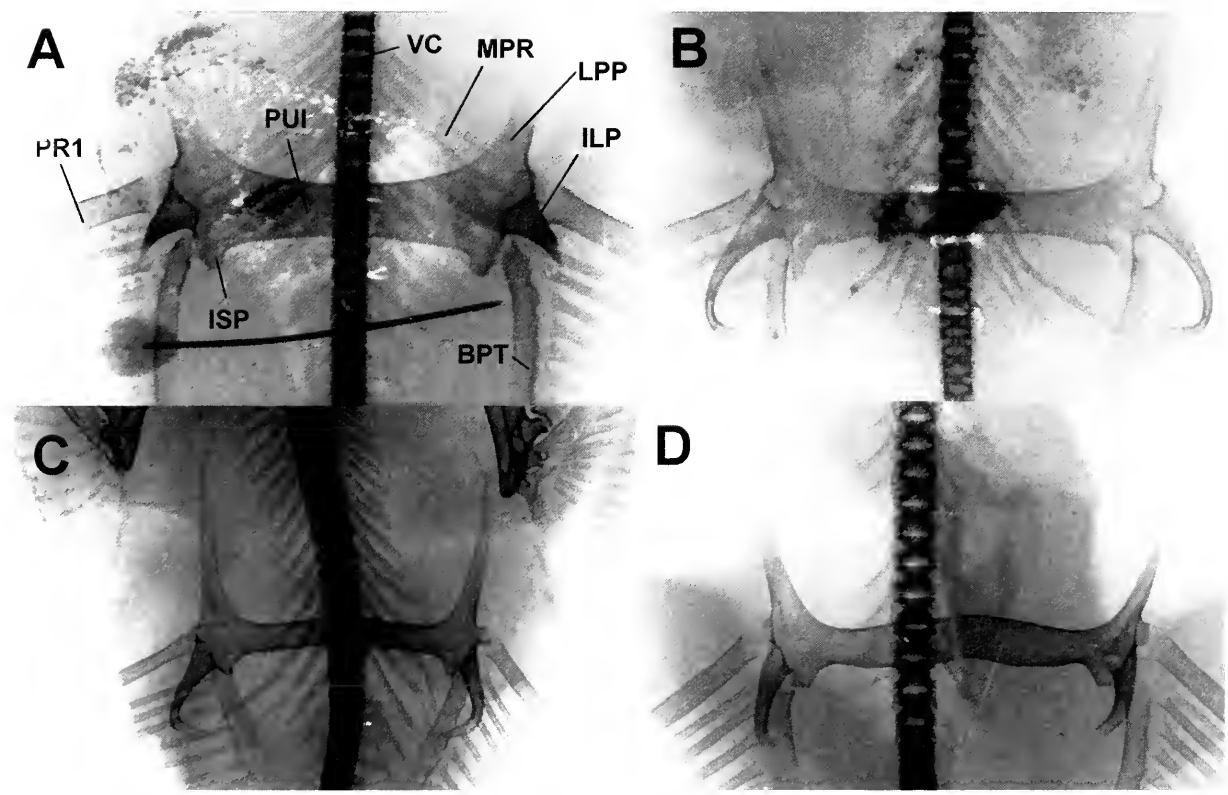

Figure 14. Narkid pelvic girdles (puboischiadic bars). **A**, *Electrolux addisoni*, holotype (note pin posterior to pelvic girdle). **B**, *Heteronarce mollis*, CAS 58351, 218 mm TL female. **C**, *Narke dipterygia*, SU-41717, female ~ 135 mm TL. **D**, *Temera hardwickii*, SU 35736, 119 mm TL, female. Abbreviations: BPT, basipterygium; ILP, iliac process; ISP, ischial process; LPP, lateral prepelvic process; MPR, ribs on monospondylous precaudal vertebrae; PR1, first pelvic fin radial; PUI, puboischiadic bar; VC, vertebral column.

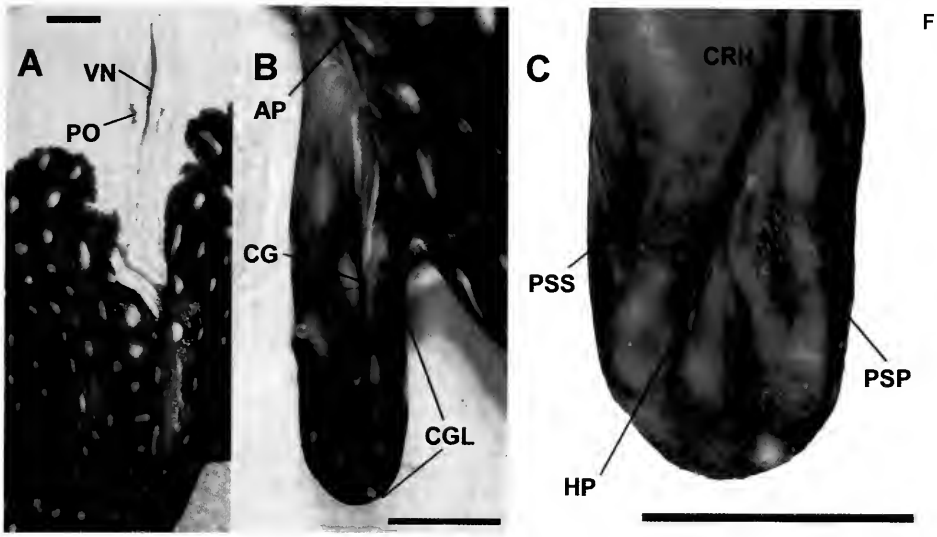

Figure 15. Claspers of *Electrolux addisoni*, paratype: **A**, claspers and vent, ventral view; **B**, right clasper in dorsal view; C, clasper glans in dorsal view. Abbre-viations: AP, apopyle; CG, clasper groove; CGL, clasper glans; CRH, cover rhipidion; HP, hypopyle; PO, abdominal pores; PSP, pseudopera; PSS, pseudo-siphon; VN, vent. Scale bars = 10 mm.

locality data in part from Koornhof, 1995). These include from southwest to northeast (Fig. 17, numbered 1-5): 1, Coffee Bay, Eastern Cape (ca. 31°58'S, 29°9'E; depth ~ 10 m); 2, Manaba Beach, the type locality near Margate (30°51.4'S, 30°23.1'E, depth 6-12 m); 3, Protea Banks, about 8 km off Shelly Beach near Margate (ca. 30°49.8'S, 30°28.8'E, depths ~ 28-35 m); 4, Aliwal Shoal, 4.8 km. off Park Rynie (ca. 30° 19.2'S, 30°48'E, depths ~ 14-30 m.); 5, Tee (or T-) Barge north of Durban and about 3 km off Virginia Beach (an artificial reef habitat at ca. 29°47'S, 31°05'E, depths ~ 20-27 m.).

Wallace's (1967) survey of electric rays from the east coast of southern Africa did not report this species. To our knowledge, this ray has not been seen south of Coffee Bay or along the south coast to False Bay. *Electrolux addisoni* was not taken by the South African Marine and Coastal Management's (MCM) research vessel *Algoa* during Cruise 014 off Mozambique in 1994 with 28 stations on soft bottom at 37-500 m depth. The *Algoa* collected torpedinoids in small numbers including *Heteronarce garmani, Narcine rierai*, and a second species of Narcine similar to the Malagasy *N. insolita* (Compagno *in* Smith & Heemstra, 1995, Compagno, 1999b, de Carvalho et al., 2002). The MCM research vessel *Africana* did not collect either *E. addisoni* or *H. garmani* in thousands of inshore and offshore bottom trawl stations at 17-200 m. during two decades of fisheries survey (ongoing) on the east coast of South Africa from Cape Agulhas to Port Alfred. However, *Narke capensis* were commonly caught by the *Africana* in this area at 27- 90 m depths (average depth 55 m) and apparently also occur in shallow inshore waters. M. Marks (*pers. comm.*) caught *N. capensis* by hand while diving at 4.5 m in False Bay in the Western Cape Province.

Electrolux addisoni occurs on the continental shelf on reefs with sandy or gravelly areas from close inshore to less than 50 m depth and including patches of appropriate habitat on inshore and offshore rocky banks and reefs. We wonder if this conspicuous ray is largely restricted to soft bottom patches on reefs off subtropical South Africa because of its having not been seen or collected elsewhere in southern Africa, including dive sites south of Coffee Bay and off Mozambique.

Conservation Status: The conservation status of this ray is uncertain but worrisome, because it is only known from a few records to date on a heavily utilized narrow strip of habitat with extensive and intensive recreational diving and sport and commercial fishing, along with runaway coastal housing development. Its known habitat and geographic distribution suggest that *Electrolux addisoni* could be at risk from human activities including harassment and disturbance by divers, as well as fisheries, pollution, and habitat degradation. There are no known fisheries that target this species or include it as bycatch, although it might become of some interest in the aquarium fish trade, and it would make a spectacular aquarium exhibit provided one could collect live specimens and keep them successfully in captivity. In terms of its known range and area 'footprint' (perhaps not more than a few square kilometers), rarity, and exposure to human activities, this species might rank high on the IUCN Red List criteria for threatened species, possibly Critically Endangered (IUCN, 2006), although there are problems with ranking it with IUCN criteria, because data on trends in abundance are non-existent. The senior author suggests that species of electric rays with limited ranges in the tropical-subtropical southwestern Indian Ocean, particularly species of insular *Torpedo* and quite possibly narkids and

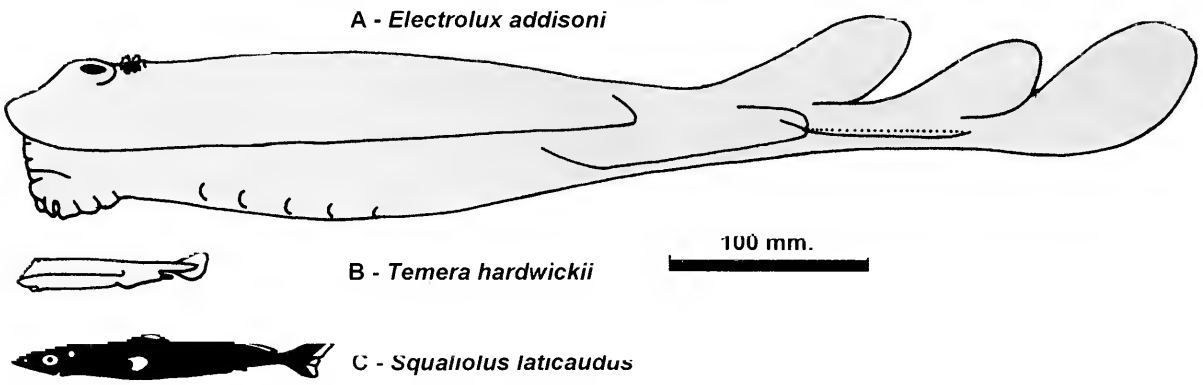

Figure 16. Size comparisons of the possibly largest narkid. A, *Electrolux addisoni* (holotype at 515 mm TL) with B, the smallest adult male examined of the diminutive narkid *Temera hardwickii* (ZRC no number, 82 mm TL) and C, the adult male holotype of the dalatiid shark *Squaliolus laticaudus* (USNM 70259, ca. 150 mm long, after Smith 1912).

Figure 17. Digital map of South Africa showing localities for *Electrolux addisoni* (filled circles) and 200 m and 1000 m isobaths. Localities are numbered from southwest to northeast (1 from Eastern Cape, 2-5 from KwaZulu-Natal): 1, Coffee Bay; 2, Manaba Beach (type locality); 3, Protea Banks; 4, Aliwal Shoal; 5, Tee Barge, north of Durban.

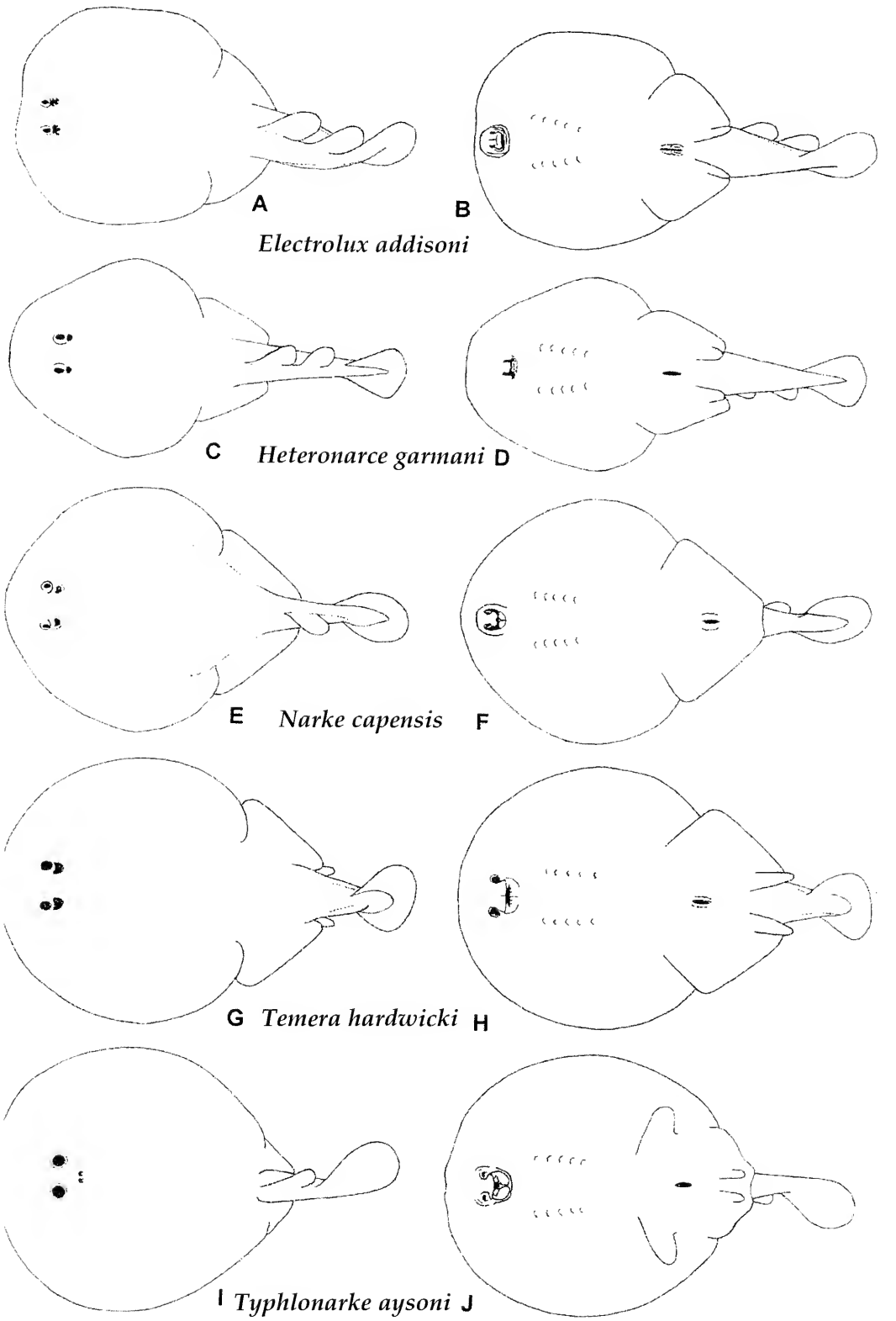

Figure 18. Dorsal (A, C, E, G, I) and ventral (B, D, F, H, J) views of A-B. *Electrolux addisoni*, holotype. C-D. *Heteronarce garmani*, 145 mm TL adolescent male, RV *Benguela* G13531 88N 30-08. E-F. Narke capensis, 231 mm TL adult female, RV *Africana* A12093 095 040 1035. G-H. *Temera hardwickii*, **SU** 35728, 104 mm TL adolescent male. I-J. *Typhlonarke aysoni*, 354 mm TL adult male. Drawings mostly by the senior author and Elaine Heemstra, I-J modified from a drawing in Garrick (1951).

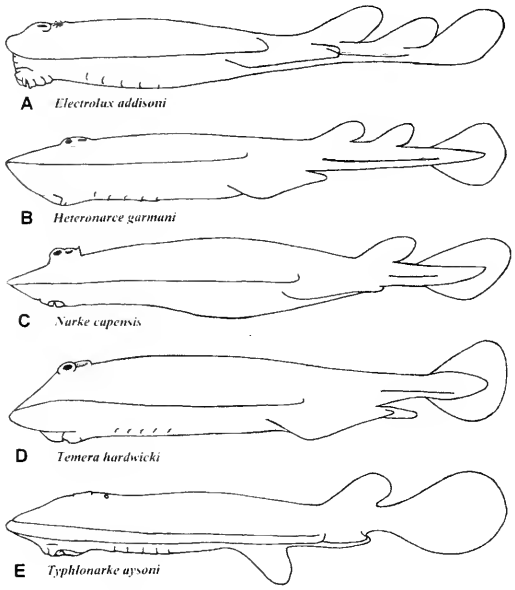

Figure 19. Lateral views of **A**, *Electrolux addisoni*. **B**, *Heteronarce garmani*. **C**, *Narke capensis*. **D**, *Temera hardwickii*. **E**. *Typhlonarke aysoni*. Same specimens and artists as in Fig. 18.

narcinids, are a major (if limited) concern for conservation, as are offshore scyliorhinid catsharks of the genus *Holohalaelurus* in the area (Human, 2006). *Electrolux addisoni* would be an appropriate subject for a dive survey project by fish-watchers, professional ichthyologists and conservationists on the numerous dive sites of the northeast coast of the Eastern Cape Province, kwaZulu-Natal and Mozambique to attempt to better understand its distribution and estimate its abundance for the purposes of assessing its conservation status.

TORPEDINOID CLASSIFICATION AND NOMENCLATURE

The classification and nomenclature of torpedinoids used here follows Gill (1862, 1895) and Compagno (1973, 1999a, 2005). For discussion in the text below, detailed data on nomenclature, authors, dates, synonymies and modern equivalents are given for torpedinoid family groups (Table 3), torpedinoid genera (Table 4), and species of Narkidae (Table 5). Citations of families, genera and species below are abbreviated by omitting the authors and dates except in formal synonymies. The electric rays (suborder Torpedinoidei or order Torpediniformes) have long been recognized as very distinct from other batoids, with a variety of classifications including a separate order Torpediniformes (eg., Compagno, 1973, 1977) or suborder Torpedinoidea or Torpedinoidei (Bigelow & Schroeder, 1953, Compagno, 2005). Discussion of the higher classification and interrelationships of torpedinoids to other batoids is not elaborated here but has been considered by many authors. Suffice it to note that in modern studies torpedinoids are always regarded as monophyletic and distinct from other batoid groups and have numerous shared derived characters not found in other batoids.

The classification of electric rays at the familial level had not varied much until the last half of the 20th Century and torpedinoids have usually been placed in a single family without subdivision. Bonaparte (1838) proposed a subfamily, Torpedinini, and Müller & Henle (1841) proposed a single family, Torpedines, for the four valid genera known at the time (*Astrape* = *Narke, Narcine, Torpedo* and *Temera*). Torpedinidae or its numerous synonyms (Table 3), were utilized by 19th Century and most 20th Century authors for all electric rays. Gill (1862) proposed the division of his family Torpedinoidae (or Narcaciontoidae) for all electric rays into three subfamilies and four subgroups (equivalent to tribes) as follows:

Subfamily Hypninae. Disc pyriform, formed by the union of the true disc with the ventrals, [pelvic fins] which are united beneath the tail; tail very short; head emarginated in front; spiracles far behind eyes; teeth with three points; dorsals [fins] two. *Hypnos.*

Subfamily Narcaciontinae. Disc and tail nearly equal; head emarginated in front; spiracles far behind eyes; teeth transverse, with one point. *Narcacion* (= *Torpedo*), with two subgenera *Narcacion* and *Tetronarce*

Subfamily Narcininae. Disc and tail nearly equally long; head entire or convex in front; spiracles close behind eyes; teeth rhombic or hexagonal.

[Tribe] Discopygae. Dorsals two, ventrals [pelvic fins] united beneath the tail; teeth rhombic, acute behind; disc orbicular. *Discopyge.*

[Tribe] Narcinae. Dorsals two, ventrals separated; teeth rhombic, with a median point. Narcine, with three subgenera *Narcine, Cyclonarce,* and *Gonionarce.*

[Tribe] Astrapae. Dorsal [fin] single. Teeth rhombic, each with a median point; disc sub-circular. *Astrape* (= *Narke*).

[Tribe] Temerae. Dorsal [fin] obsolete; teeth hexagonal and flat; disc sub-circular. *Temera.*

Gill (1893) mentioned the division of his family Torpedinidae into three subfamilies, Torpedininae, Narcininae and Hypninae with tribes and generic allocations not specified. Fowler (1934, 1941) proposed the division of the family Torpedinidae into three subfamilies based on presence and number of dorsal fins, as with Gill's (1862) tribal classification within his Narcininae, but with the union of two-dorsal fin taxa in subfamily Torpedininae for *Narcine, Heteronarce, Benthobatis, Hypnos* and *Torpedo*; subfamily Narkinae for the one-finned Narke (including *Bengalichthys*) and

Typhlonarke, and subfamily Temerinae for the finless *Temera*.

Bigelow & Schroeder (1953) followed Fowler's classification but raised the rank of his subfamilies to family (Temeridae, Narkidae, and Torpedinidae) and added *Discopyge* and *Diplobatis* to the Torpedinidae. Their classification was followed by a few subsequent authors, including Lindberg (1971) and Rass & Lindberg (1971). Bigelow & Schroeder (1953: 86) cautioned that Fowler's system based on the number of dorsal fins was artificial, and that it ran "counter to a dichotomous grouping based on the firmness of articulation of the upper and lower jaws and the presence or absence of labial cartilages, characters which are probably of greater importance phylogenetically than the number of dorsal fins." Bigelow and Schroeder retained Fowler's arrangement as a matter of convenience, as being appropriate to a general work, and because several of the torpedinoid genera had not been examined for jaw morphology. They expected that a torpedinoid classification based on jaw morphology would eventually replace the dorsal fin scheme.

Fowler (1970) retained a single family Torpedinidae but included a modified arrangement of five subfamilies with a somewhat different composition than his earlier work and apparently incorporating elements of Gill's (1862) arrangement: Temerinae for the no dorsal fin *Temera;* Narkinae for the one-dorsal *Narke, Typhlonarke* and *Bengalichthys* (= *Narke*); Discopyginae for the two-dorsal *Discopyge;* Hypninae for the two-dorsal *Hypnos;* and Torpedinidae for the one-dorsal *Crassinarke* (= *Narke*) and two-dorsal genera *Benthobatis, Diplobatis, Heteronarce, Narcine,* and *Torpedo.*

Compagno (1973, 1977, fig. 12) proposed a revised classification of the electric rays based on anatomical comparisons of members of all the torpedinoid genera. The torpedinoids were divided into two well-defined superfamilies, Torpedinoidea and Narcinoidea, that verified and expanded the alternate dichotomous arrangement suggested by Bigelow & Schroeder (1953) as follows:

Superfamily Narcinoidea: Mouth straight, with stout jaws; strong labial cartilages; rod-shaped hyomandibulae; well-developed ceratohyals; branched, antler-like antorbital cartilages; short and broad crania; well-developed frontoparietal fenestrae; rostrum present; occipital condyles not exserted; and disc rounded anteriorly. Families Narcinidae and Narkidae.

Family Narkidae: shallow groove around mouth; narrow, rod-shaped rostrum; nasal capsules anteroventrally directed, contiguous, with a narrow internasal plate; precerebral fossa very small and terminated anteriorly by abrupt constriction of the rostrum; jaws short, stout and weakly protrusile; anterior hypobranchial elements and ceratohyals enlarged; posterior hypobranchials narrow and separated from each other by a wide space; and basibranchial copula small. Genera: *Heteronarce, Narke, Temera,* and *Typhlonarke.*

Family Narcinidae. Deep groove entirely surrounding mouth and lips; rostrum broad, trough or shovel shaped; nasal capsules directed ventrolaterally, separated by a wide, flat internasal plate; precerebral fossa very large; jaws long, stout, and strongly protrusile; anterior hypobranchial elements and ceratohyals small; posterior hypobranchials very broad and nearly meeting mid-ventrally; and basibranchial copula moderately large. Genera: *Benthobatis, Diplobatis, Discopyge,* and *Narcine.*

Superfamily Torpedinoidea: Mouth arcuate, very extensile, with extremely slender jaws; no labial cartilages; flattened triangular hyomandibulae; no ceratohyals; pinnate antorbital cartilages; crania elongated and narrow; with poorly developed frontoparietal fenestrae; rostrum absent or reduced; occipital condyles exserted; disc truncate and emarginate anteriorly. Families: Hypnidae and Torpedinidae.

Family Hypnidae. Disc pear-shaped, tail rudimentary with two tiny dorsal fins and a small caudal fin; teeth tricuspid; "rostral appendices" articulating with cranium (Haswell, 1885); ethmoid region strongly bent ventrally, with nasal capsules expanded anteroventrally, contiguous, internasal plate narrow and compressed, not separating nasal capsules; preorbital processes absent; otic capsules large, with their outlines expanded abruptly from orbital walls; and one pair of hypobranchials articulating with basibranchial copula. Genus *Hypnos.*

Family Torpedinidae. Disc subcircular, tail well-developed, with two moderate-sized dorsal fins and large caudal fin; monocuspid teeth; "rostral appendices" (Holmgren, 1941) fused to cranium; ethmoid region not bent ventrally, nasal capsules expanded laterally and separate, internasal plate wide and flat; preorbital processes present; otic capsules small, their lateral surface sloping gradually into orbital walls; two pairs of hypobranchials articulating with basibranchial copula. Genus *Torpedo.*

This four-family torpedinoid classification was utilized by several authors including McEachran & Compagno (1982), Carroll (1988), Compagno (1990, 1999a,b, 2005), Last & Stevens (1994), McEachran *et al.* (1996), Compagno & Last (*in* Carpenter & Niem, 1999a, b, c), Compagno *et al.* (*in* Carpenter & Niem, 1999), and Carvalho *et al.* (*in* Carpenter & Niem, 1999). 'Downranked' variants of this classification include Nelson (1976, 1984) with a single family Torpedinidae and two subfamilies: Torpedininae and Narcininae with two tribes each. Torpedininae has the tribes

Torpedinini and Hypnini while Narcininae has the tribes Narcinini and Narkini. Nelson (1994) modifies these to two families (Torpedinidae and Narcinidae) with two subfamilies each. Zhu & Meng (1979) used the families Torpedinidae and Narkidae for the two main groups, while Eschmeyer (1990, 1998) used two families Torpedinidae and Narcinidae. Shirai (1996) used one family Torpedinidae and three subfamilies, Torpedininae for *Hypnos* and *Torpedo*, Narkinae for the narkids *Heteronarce, Narke, Temera,* and *Typhlonarke,* and Narcininae for *Benthobatis, Diplobatis, Discopyge,* and *Narcine.*

Our comparison of narkid genera with one another and with other torpedinoids reinforces the distinctiveness of the four families and their grouping into two higher groups (superfamilies) which corresponds to morphological similarities that reflect very different trophic specializations in the two superfamilies. Torpedinoidea feed on large prey that are stunned by the electric organs and swallowed whole through their distensible (snake-like) mouths and flexible jaws. Narcinoidea are bottom feeders that use their more or less protrusible jaws to feed on small prey on or in the substrate. Both groups can use their electric organs defensively against predators, but their utility in feeding is uncertain among the Narcinoidea. A detailed review of torpedinoid systematics and interrelationships of the families and a revision of the Narkidae (particularly *Narke* including describing new species) are needed, but these tasks are beyond the scope of this paper and more appropriate elsewhere. The present work concentrates on the systematics of *Electrolux* but has revealed numerous additional characters distinguishing the genera of Narkidae and provides materials for a future cladistic analysis of the genera that would be preliminary and inappropriate here without a revision of the family.

KEY TO TORPEDINOID FAMILIES

Key modified from Compagno *et al.* (*in* Carpenter & Niem, 1999)

1a. Mouth broadly arcuate, protrusile and greatly distensible; no labial folds and cartilages at corners of mouth.....**2**

1b. Mouth nearly straight, more or less protrusile but not much distensible; strong labial folds and cartilages at corners of mouth **3**

2a. Disc longer than wide, heart or pear-shaped; teeth tricuspid; tail much reduced; caudal fin about as high as dorsal fins .....**Hypnidae**
(Australia)

2b. Disc transversely elliptical, not pear-shaped; teeth monocuspid; tail not greatly reduced, caudal fin much higher than dorsal fins
.....**Torpedinidae**
(Wide-ranging in all temperate and tropical seas)

3a. Snout firm, with broad, stiff, shovel-shaped rostral cartilage, readily felt by palpitation of snout; deep groove around mouth; teeth extending onto outer surfaces of jaws in most species .....**Narcinidae**
Wide-ranging in most temperate and tropical seas except for Eastern Atlantic.

3b. Snout soft, with a slender, rod-shaped rostral cartilage; shallow groove around mouth; teeth not extending onto outer surfaces of upper and lower jaws.....**Narkidae**.
(Eastern South Atlantic and temperate and tropical Indo-West Pacific from South Africa and Red Sea to Indonesia, Japan and New Zealand)

FAMILY NARKIDAE FOWLER, 1934. SLEEPER RAYS

Group Astrapae Gill, 1862: 387 (Family Torpedinoidae or Narcaciontoidae, subfamily Narcininae Gill, 1862). Type genus: *Astrape* Müller & Henle, 1837 (= Narke Kaup, 1826). Proposed as a group that is equivalent to tribe in rank for purposes of nomenclature.

Subfamily Narkinae Fowler, 1934: 240 (Family Torpedinidae). Type genus: *Narke* Kaup, 1826. Replaces Astrapae Gill, 1862. Family Narkidae Bigelow & Schroeder, 1953: 87; and Narkidae Compagno, 1973: 41.

Group Temerae Gill, 1862: 387 (Family Torpedinoidae or Narcaciontoidae, subfamily Narcininae). Type genus: *Temera* Gray, 1831. Subfamily Temerinae Fowler, 1934: 240 (Family Torpedinidae), Family Temeridae Bigelow & Schroeder, 1953: 87. Compagno (1973: 41) synonymized Temeridae with Narkidae although Temerae Gill, 1862 has priority.

FAMILY DIAGNOSIS (derived and expanded from Compagno, 1973, 1977, 1999a and Compagno & Last *in* Carpenter & Niem, 1999a): Electric rays with short preorbital snouts, 5-13% TL; snout broadly rounded anteriorly or nearly truncate (*Electrolux* and some *Heteronarce* species). Spiracles contiguous with posterior edges of eyeballs, not situated behind them; margins of spiracles usually smooth and flat or with a low ridge, elevated and occasionally with a few low papillae in *Narke capensis,* or with several long and prominent papillae that screen the spiracles (*Electrolux*). Nasal curtain elongated, narrow, posteriorly expanded and thickened, with prominent ampullal pores on its ventral surface. Mouth transverse, small and narrow, not highly distensible; shallow circumoral groove surrounding mouth and lips; labial folds and grooves strong. Tooth row counts low, 8-17 / 7-21 or 15-38 total rows; teeth concealed when mouth is closed; teeth small, rounded-oval, unworn crowns with keels or a single low blunt, broad cusp. Tail fairly large and stout but variably short to moderately elongated. Disc circular, ovate, rounded-

angular or pear-shaped, often about as broad as long. Pectoral girdle crescentic; tubular section of lateral faces of scapulocoracoids greatly elongated, longer than medial fenestrated section. Suprascapulae V- or C- shaped, with fused midline above free vertebrae behind synarcual. Superscapulae articulating with scapulae entirely in front of coracoid bar or crossing above bar. Metapterygial axis subequal to propterygial axis or much shorter; propterygial radial count equal to metapterygial radial count or much more numerous. Puboischiadic bar with prominent short to greatly elongated iliac processes. Two dorsal fins (*Electrolux, Heteronarce*) or one dorsal fin (*Narke, Typhlonarke*) , or dorsal fin absent (*Temera*). Caudal fin larger than dorsal fins or fin (when present) and subequal to or somewhat smaller in size than pelvic fins (*Typhlonarke* with pelvic fins fused to disc); caudal fin without prominent ventral lobe. Cranium short and fairly broad; rostrum incomplete, medial floor reduced to narrow medial rostral cartilage and paired lateral rostral cartilages below it, lateral walls of rostrum truncated around precerebral cavity and fused to ethmoid region of cranium; medial rostral cartilage rod-shaped with short bifurcated rostral node, less than one-third nasobasal length. Rostral appendices small, separate from rostrum, just lateral to rostral node, and articulating with antorbital cartilages. Precerebral fossa very small and terminated anteriorly by an abrupt constriction of the lateral walls of the rostrum. Ethmoid region anteriorly directed or strongly bent ventrally (*Electrolux*); nasal capsules expanded anteroventrally or laterally; nasal cartilages (ala nasalis) greatly expanded posterolaterally from the nasal capsules to support the expanded and thickened nasal curtain; internasal plate narrow, compressed, narrowly separating the nasal capsules. Antorbital cartilages more or less branched and antler-like (narrower distally in *Electrolux* and in *Heteronarce garmani* than in other narkids examined); bases of cartilages articulating on posterolateral surfaces of nasal capsules; shafts of cartilages directed more or less anterolaterally; a lateroposteriorly directed spur or process present or absent on shafts of antorbital cartilages. Preorbital processes apparently absent. Cranial roof perforated by frontoparietal fenestra (*Narke, Temera, Typhlonarke*) or not (*Electrolux, Heteronarce*); when present long, U-shaped and contiguous with anterior fontanelle or separated from it by an epiphysial bridge. Otic capsules large and broad, length about 33-40% of nasobasal length, width across capsules about 59-68% of nasobasal length, capsules rather inflated and expanded laterally, distally rounded-angular; lateral outlines of otic capsules sloping gradually into orbital walls. Occipital condyles relatively short and low, not strongly exserted from occiput. Jaws stout and transverse, weakly protrusile. Palatoquadrates thick, straight and subtriangular, with strong overlapping processes on their articulation with Meckel's cartilages; orbital cartilages obsolete to strong on palatoquadrates. Meckel's cartilages very stout, flat and broad, strongly expanded symphysially and distally, with a weak to strong distal process. A large flat oval mental cartilage just posterior to lower symphysis in most genera (possibly absent in *Typhlonarke*). Well-developed upper and lower labial cartilages present and close to symphyses, dorsal labial cartilage simple or forked. Hyomandibulae heavy, elongated and sigmoid-shaped, with expanded bases and apices; ceratohyals well-developed and large, about size of anterior hypobranchials. Prespiracular cartilages present but postspiracular cartilages absent. Two pairs of hypobranchials, the posterior pair articulating with basibranchial copula; anterior hypobranchials large, as broad or broader than posteriors but not as long; posterior hypobranchials broad to very narrow and separated from each other by a narrow (*Electrolux*) to wide space (*Narke, Temera,* with *Heteronarce* intermediate). Basibranchial copula small and tack-shaped (*Narke* and *Temera*), larger and more rounded-angular in *Electrolux* and apparently *Heteronarce*. Dorsal surface usually brownish or reddish-brown, white or brownish below; dorsal surface either plain or with a few large dark spots or blotches, paired white spots, and white side bands on the tail and posterior pelvic bases, usually without a complex colour pattern or ocelli on pectoral fins (*Electrolux* exceptional with its elaborate colour pattern). Dwarf to moderate-sized batoids, adult males 82-515 mm TL and possibly longer (see size discussion for *Electrolux*, above).

Genera of Narkidae and status of Heteronarce: *Heteronarce, Narke, Temera,* and *Typhlonarke* were included in the Narkidae (Compagno, 1973), to which we add *Electrolux* as the second genus of two-dorsal narkid. We initially considered *Electrolux addisoni* as a possible species of *Heteronarce* but it soon became apparent that it was very different from any species of *Heteronarce* and that the four valid species of *Heteronarce* formed a coherent genus that is separable from *Electrolux* and other narkids. We present meristic data of *Heteronarce* and other narkids (Tables 6, 7 & 8) and morphometric data (Table 9) for *Heteronarce* and and can easily distinguish *Electrolux* and *Heteronarce* from each other and from other narkids. Figures 18 and 19 summarize external differences within narkid genera, Figures 6 and 7 show differences in mouth and nostril structures, Figures 5, 9, 10, 11 and 12 differences in head anatomy, Figure 13 pectoral girdle structure and Figure 14 pelvic girdle structure.

There has been considerable confusion in the literature on the status, familial position, and species of *Heteronarce*. Some authors have doubted its distinction from *Narcine* and have synonymized the two genera or have mistaken species of *Heteronarce* for *Narcine* or *vice versa*. Part of the problem is that

Heteronarce was originally defined on a few nasoral characters that although partially valid were not seen as definitive by some authors, particularly after a few species of Narcine were discovered with elongated, relatively narrow, *Heteronarce*-like nasal curtains.

The first valid species of *Heteronarce* was described by Lloyd (1907) as *Narcine mollis* from the Gulf of Aden at 238 m. This was distinguished from the Indian species *N. timlei* by its enlarged anterior nasal valves (circumnarial folds) and more elongated nasal curtains about as long as wide (about three times wider than long in *N. timlei*). Lloyd (1909) and Annandale (1909) gave additional information on *N. mollis* including illustrations of the whole ray, teeth, and oral anatomy. Garman (1913) included *N. mollis* in *Narcine* without comments.

The genus *Heteronarce* was proposed by Regan (1921) for a second new species of two-dorsal electric ray, *H. garmani*, collected about 15-22 miles off the Umvoti River, kwaZulu-Natal, South Africa, in 120-130 fms depth, and for *Narcine mollis* Lloyd, 1907. *Heteronarce* was distinguished from *Narcine* by "the minute nostrils, the length of the anterior nasal valves, which are confluent to form a curtain that is not much broader than long and is studded with pores, and the lateral position of the posterior nasal valves." (Regan, 1921). Regan noted that *H. garmani* was very similar to *H. mollis* but had much smaller eyes and spiracles, a longer snout, a smaller mouth and nasal valves, and different coloration (brown above and white below in *H. garmani*, dark brown above and gray-brown below in *H. mollis*). Regan did not assign a type species for *Heteronarce*, but this was subsequently designated as *H. garmani* by Fowler (1941).

Von Bonde & Swart (1923) described a third species, *Heteronarce regani* from a 190 mm specimen from kwaZulu-Natal, South Africa (two stations mentioned, depth 211-329 m), but didn't compare or distinguish it from *H. garmani* which they also recognized. Their specimen (pl. 22, fig. 2) had a truncated caudal fin tip that is unusual compared to the rounded caudal tips of other *Heteronarce* species and might be abnormal. The genus *Heteronarce* was not characterized by these authors.

Fowler (1925a) described a fourth species of *Heteronarce* as *Narcine natalensis*, from a 260 mm specimen trawled from off kwaZulu-Natal at 40 fathoms, but didn't refer to Regan's or von Bonde & Swart's accounts and didn't compare it with either *H. garmani* or *H. regani*. Fowler (1925b) subsequently synonymized his *N. natalensis* with *H. garmani*, and later (Fowler, 1941) included both *N. natalensis* and *H. regani* in synonymy of *H. garmani*. Fowler's (1941) synonymy was recognized by Wallace (1967) and is followed here. Fowler (1941) included *H. mollis* and *H. garmani* in *Heteronarce* and separated this genus from *Narcine* by its more elongated nasal curtain.

Bigelow & Schroeder (1953) included *Heteronarce* and *Narcine* in their Family Torpedinidae as separate genera, but noted that *Heteronarce* (including *H. garmani* and *H. mollis*) was so close to *Narcine* that its generic validity was doubtful, and differed only in its more elongated nasal curtain. However Compagno (1973) noted that *Heteronarce* "had two dorsals, and had usually been placed in the vicinity of Narcine, but examination of its exterior and skeleton revealed its affinity with *Narke*.

McKay (1966) described *Narcine westraliensis* from Western Australia which has an unusually elongated nasal curtain for a narcinid that resembles that of *Heteronarce*. McKay used this similarity to synonymize *Heteronarce* with *Narcine*. However, the chondrocranium and oral structure of *N. westraliensis* as described by McKay is like that of other *Narcine* species and of narcinids and unlike that of *Heteronarce* and other narkids.

Talwar (1981) reviewed *Heteronarce* and named a fifth species from the southwest coast of India, *H. prabhui*. Talwar recognized three valid species, including *H. garmani* from southern Africa (with synonyms *H. regani* and *Narcine natalensis*), *H. mollis* from the Arabian Sea, and *H. prabhui* from India. Talwar defined *Heteronarce* as having the disc rounded anteriorly, a shallow groove around the mouth, jaws short and weakly protractile, eyes well developed and almost contiguous with spiracles, nasal curtain only slightly broader than long, and two dorsal fins.

Baranes & Randall (1989), described *Narcine bentuviai* from 80-200 m. in the Gulf of Aqaba, Red Sea, which proved to be a sixth and unusual species of *Heteronarce*. *Heteronarce bentuviai* has a unique bold and black-blotched color pattern and a second dorsal fin noticeably smaller than the first dorsal. *H. mollis*, *H. garmani*, and *H. prabhui* in contrast are uniformly colored and have second dorsal fins about as large as the first. According to Baranes & Randall's detailed account, the external morphology and anatomy of *H. bentuviai* agrees with that of other narkids and particularly with other species of *Heteronarce* but not with *Narcine* or other narcinids. These authors tentatively placed their species in *Narcine* because they considered *Heteronarce* a junior synonym following McKay (1966), but noted that an alternate generic arrangement might remove it from Narcine. De Carvalho (1999) excluded *H. bentuviai* from *Narcine* in his revision of the genus.

Lloris & Rucabado (1991) described a seventh species, *Heteronarce rierai* from off Mozambique, but this proved to be a narrow-bodied *Narcine* with a narrow nasal curtain as in *N. westraliensis* but like that species has mouth and anatomical characteristics typical of narcinids (Compagno, *in* Smith & Heemstra, 1995, de Carvalho, 1999). There are several other narrow-bodied species of *Narcine* in Australian waters (MacKay, 1966, Last & Stevens, 1994, de Carvalho, 1999).

The superficial external similarity of *Heteronarce* to *Narcine* is contradicted by its anatomical and external

differences (particularly in the oral and chondrocranial morphology) which are similar to those of other narkids rather than *Narcine* or other narcinids. Based on our examination of *Heteronarce* specimens, as well as literature data, we confirm that *Heteronarce* is a valid and well-defined genus including the four species *H. bentuviai, H. garmani, H. mollis,* and *H. prabhui,* with the latter species morphologically very similar to *H. mollis*. *Heteronarce* is separable from narcinids by characters in the key to families and definition of the Narkidae above, and separable from other narkids in the key to narkid genera and in comparison with *Electrolux*.

KEY TO NARKID GENERA

1a. No dorsal fins.....***Temera***
(Indo-West Pacific from Andaman Sea near southern Thai-Burma border through Straits of Malacca and Malay Peninsula to Singapore, Thailand and Viet-Nam, doubtful from Philippines)

1b. One or two dorsal fins 2

2a. One dorsal fin.....3

2b. Two dorsal fins 4

3a. Eyes not visible externally; anterior lobes of pelvic fins form isolated leg-like structures protruding from ventral surface of pectoral disc, posterior lobe of pelvic fins fused to pectoral disc .....***Typhlonarke***
(New Zealand)

3b. Eyes usually visible externally; no separate pelvic fin lobes .....***Narke***
(Southeastern Atlantic and Indo-West Pacific, South Africa, northern Arabian Sea, India, Malaysia, Singapore, Indonesia, Thailand, Viet-Nam, Philippines (doubtful), China, Taiwan, Japan, Korea)

4a. Spiracles with long, slender, stiff papillae (Fig. 5A); nostrils and mouth projecting ventrally as prominent nasoral turret near front of disc (Figs 3B; lower lips thin, without a chin (mental) groove and with labial cartilages not meeting at midline (Fig. 7A & 12A); tooth rows numerous, 32-34 total; dorsal side of disc with numerous pale spots on dark brown background, live ray with elaborate concentric pattern of black lines and pale spots; underside of disc white medially, the broad distal margin dark brown, with numerous small pale spots .....***Electrolux***,
(Western Indian Ocean, South Africa)

4b. Spiracles without papillae (Fig. 5B); nostrils and mouth not projecting as a prominent nasoral turret at front of disc, more posterior and slightly projecting from ventral surface of disc; lower lips thick, with prominent mental groove and labial cartilages meeting at symphysis (Figs 7B & 12B); tooth rows fewer, 20-24 total; uniform pale to dark brown or grayish above, without markings or with a few large black blotches on disc, first dorsal fin and caudal fin, white, grayish or gray-brown below .....***Heteronarce***
(Western Indian Ocean, South Africa to Gulf of Aqaba, Arabian Sea and west coast of India)

MATERIAL EXAMINED

INSTITUTIONAL ABBREVIATIONS: Institutional abbreviations for specimens of Narkidae mostly follow Compagno (1988): **BMNH** - Natural History Museum, London, UK, formerly British Museum (Natural History). **CAS** - California Academy of Sciences, San Francisco, California, USA. **GVF** - George Vanderbilt Foundation fish collection, Stanford University, Stanford, California, USA, housed at the California Academy of Sciences. **ISH** - Institut für Seefischerei, Hamburg, Germany. **KUMF** - Kasetsart University. Faculty of Fisheries, Museum, Bangkok, Thailand. LJVC - XXXX and **LJVC** - YYMMDD (Year, Month, Day), L.J.V. Compagno accession number and field-accession number. **PCH** - Phillip C. Heemstra field numbers. **NMS** - National Museum of Singapore (formerly Raffles Museum) zoology collection, housed in the Department of Zoology, National University of Singapore. **SAIAB** - South African Institute of Aquatic Biodiversity, formerly **RUSI**, for the J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa. **SAM** - Iziko - South African Museum, Natural History Division, department of Marine Biology, Cape Town, South Africa. **SIO** - Scripps Institution of Oceanography, La Jolla, California, USA. **SU** - Stanford University fish collection, Stanford, California, USA, housed at the California Academy of Sciences. **USBCF** - United States Bureau of Commercial Fisheries, Department of the Interior field number. Now US National Marine Fisheries Service, Department of Commerce. **ZRC** - Zoological Reference Collection, Department of Zoology, National University of Singapore.

COMPARATIVE MATERIAL - FAMILY NARKIDAE

'Crassinarke dormitor' (? = Narke japonica), **SIO** 4-257-6B, 278 mm TL adult male, Yellow Sea.

Heteronarce garmani: **BMNH** 1921.3.1.3, holotype, adult male, 169 mm TL, 77 mm DW, 1921, Umvoti River, kwaZulu-Natal, South Africa, 220-238 m. **SAM** 34813, two adult males, 256-289 mm TL and 124-135 mm DW, RV Algoa, C00813 014 011-3115, 19940612, Western Indian Ocean, Mozambique, 23° 28.0′ S, 35°43.00′ E, 185 m. **SAM** uncataloged, two females, 125-132 mm TL and 65-72 mm DW, adolescent male, 145 mm TL and 64 mm DW, RV Benguela G13531 88N 30-08, 19880822, kwaZulu-Natal, South Africa, 29°44.0′ S, 31°23.00′ E, 154 m.

Heteronarce mollis: **CAS** 58352, 206 mm TL, 92 mm DW adult male, RV Anton Bruun, AB 9-444, 19641216, N. Indian Ocean, Somalia, 9° 36.00′N, 51° 1.00′E, 78-82 m. **CAS** 58351, 6 females, 217, 226, 255, 218, 211 and 212 mm TL, 115, 120, 122, 111, 108 and 100 mm DW, 2 adult males, 220 and 199 mm TL, 118 and 100 mm DW; immature male, 165 mm TL and 90 mm DW, RV Anton Bruun, AB 9-464, 19641218, N.

Indian Ocean, Somalia, 11° 37.00'N, 51° 27.00'E, depth? **ISH** 254/75, adult male, 199 mm TL, 100 mm DW, Dr. F. Nansen, FAO, 19750303, North coast, N. Indian Ocean off Somalia, 11°41.00' N, 51°36.00'E, 82 m.

Narke capensis: (all from South Africa): *Africana* A04752 048 030-1039, immature males, 87, 94, 98 mm TL, 52, 53, 57 mm DW, adult males, 206, 250 mm TL, 142, 165 mm DW, immature female, 89 mm TL, 49 mm DW, adult (?) females, 205, 215, 223, 233, 255 mm TL, 133, 133, 137(?), 153, 164 mm DW, adult females, 193, 208, 220, 220, 224, 232, 234, 245 mm TL, 120, 139, 136, 145, 146, 156, 146, 173 mm DW, 19860920, southeastern Cape coast, , 34°16.0' S, 22°1.0'E, depth 42 m. Africana A04770 048 043-1093, adult males, 176, 237, 245 mm TL, 119, 153, 154 mm DW, immature female (?), 155 mm TL and 101 mm DW, females, 145, 165, 171, 192, 218 mm TL, 96, 108, 105, 128, 140 mm DW, 19860923, southeastern Cape coast, , 33°48.0'S, 26° 7.0' E, depth 56 m. Africana A06215 056 023-1042, adult males, 243 and 253 mm TL, 154 and 153 mm DW, adult females, 196 and 213 mm TL, 115 and 120 mm DW, 19870917, southeastern Cape coast, , 34°7.0'S, 22° 15.0'E, depth 40 m. Africana A07115 063 011-2123, adult male 243 mm TL and 172 mm DW, 19880513, southeast Cape coast, 34°30.0'S, 21°14.0'E, depth 59 m. Africana A07116 063 012 2132, male (adult?) 253 mm TL, 155 mm DW, 19880513, East coast cruise, Cape coast, 34°31.0'S, 21°17.0'E, depth 58 m. *Africana* A07128 063 020-1039, immature female, 118 mm TL, 75 mm DW, adult females, 225, 229, 246, 254, 263 mm TL, 136, 143, 156, 162,169 mm DW, adolescent male, 257 mm TL, 168 mm DW, adult males, 243, 253 mm TL, 173 mm DW (253 mm TL), 19880515, southeastern Cape coast, 34°16.0'S, 22°1.0'E, depth 35 m. *Africana* A07152 063 038-1093, adult males, 175, 178, 215, 255 mm TL, 117, 123, 134, 170 mm DW, adult females, 155, 175 mm TL., 95, 112 mm DW, 19880519, southeastern Cape coast, 33°45.0'S, 26°5.0' E, depth 32 m. *Africana* A13339 102 014-2332, immature male 73 mm TL, 50 mm DW, 1992040, southeastern Cape coast, 33°53.0'S, 26°46.0'E, depth 90 m. *Africana* A16338 122 043-1042, immature male, 105 mm TL, 68 mm DW, adult female, 176 mm TL, 109 mm DW, 19940618, eastern Cape coast, 34°9.0'S, 22°13.0'E, depth 39 m. **SAM** 34347, adult male, 174 mm TL, 118 mm DW, *Africana* A18168 135 077-1090, 19960429, southeastern Cape coast, , 33°45.0'S, 26°1.0'E, depth 27 m. depth. **LJVC** 961014, **SAM** uncataloged, adult male, 265 mm TL, 180 mm DW, M. Marks site 1, 19961013, Buffels Bay, False Bay, Western Cape, , 34°19.06'S, 18° 27.75'E, depth 4.5 m. **RUSI** 11932, adult male, 195 mm TL, 115 mm DW , TBD-3, off Swartkops, Eastern Cape, . **SAM** 22796, female, 188 mm TL, 120 mm DW, 19590919, Algoa Bay, Eastern Cape, . **SAM** 22799, female 170 mm TL, 101 mm DW, 19590916, Sandy Point, Mazeppa Bay, Eastern Cape, 32°27.00'S, 28°39.00'E. **SAM** 30992, adult male, 239 mm TL, 156 mm DW, 19781103, Muizenberg, False Bay, Western Cape.

Narke dipterygia: **BMNH** 1909.7.12.13, female, 121 mm TL, 57 mm DW, sy**ntype** of *Bengalichthys impennis* Annandale, 1909, Balasore Bay, Orissa coast, India. **CAS** uncataloged, female ca 120 mm TL, 50 mm DW, Indo-West Pacific. **CAS** 66840, female, 146 mm TL, 78 mm DW, collected by J. Mee, 19890222, Sudah, Oman, 6 m depth. **LJVC** 0508, five females, 170, 150, 150, 162 and 155 mm TL, immature male, 165 mm TL, F. Steiner, 19751006, Taiwan straits?, Taiwan. **LJVC** 0514, 157 mm TL adult (?) female, F. Steiner, 19751006(?), Taiwan straits, Taiwan? **LJVC** 0515, adult (?) females, 146 and 151 mm TL, F. Steiner, 19751006, Taiwan straits, Taiwan(?). J. Randall uncataloged, female, 131 mm TL, India. **NMS** 3119, adult males, 150 and 131 mm TL, 84 and 70 mm DW, A. K. Tham, 1964, Fisheries Biology Unit, SPR 425, Singapore. **SU** 32406, adult male, ca. 135 mm TL, 65 mm DW, India. **SU** 41717, adult male ca 150 mm TL and female ca 135 mm, India. **USBCF** F.H. Berry no number, two adult males, 170 and 180 mm TL, five females, 178, 153, 166, 130, 153 mm TL, Porto Novo, Madras, India. **USBCF** F.H. Berry, SOSC-381, female ca 160 mm TL, Porto Novo, Madras, India, 15-22 m. depth,

Narke cf. dipterygia, **KUMF** 2464, female, 120 mm TL, 75 mm DW, 19740105, Samut Songkram, Thailand,. **KUMF** 0807, female, 123 mm TL, 69 mm DW, 1968, collected by P. Wongrat, Prachuat Khiri Khan, Gulf of Thailand, **KUMF** 0834, females 109, 114 and 112 mm TL, 64, 66, 66 mm DW, 1972021-10, collected by P. Wongrat, offshore near Sataheys, Gulf of Thailand.

Narke japonica: **CAS** Acc. 1972:1:5, female, 233 mm TL, 19711200, East. China Sea, between Japan and Korea. **GVF** Naga 60-61 (**GVF**-2077), adult male ca 225 mm, 19600227, South China Sea, 15°40.00'N, 109°25.50'E. **PCH** Jan. 1988, female 168 mm TL, 93 mm DW, 1988, from Tachi, South China Sea, Taiwan. **SU** 3363, adult male, ca. 365 mm TL, Japan. **SU** 61723, female ca 215 mm TL, Japan. **SU** 7267, adolescent male, ca 195 mm TL, Japan.

Narke spp. **CAS** Acc 1972-XII: 18, immature male, 67 mm TL, adolescent males, 94 and 109 mm TL, adult males, 99 and 103 mm TL, females, 58 and 93 mm TL, southwest of Kao Ksiung, Taiwan. *Anton Bruun*, AB 4B-263, immature male, 100 mm TL, adult males, 143 and 147 mm TL, females, 117, 121, 127, 127, 132, and 139 mm TL, Arabian Sea, 22°54'N, 68°06'E. **GVF**-2430, female ca 150 mm TL, Gulf of Thailand, Thailand. **GVF**-2449, adult males, 153 and 154 mm TL, female, ca. 125 mm TL, Gulf of Thailand, Thailand. **GVF**-2663, female ca 150 mm TL, Gulf of Thailand, Thailand. **CAS** *Anton Bruun* AB 4B-223A, females, 130, 150 and 165 mm, Arabian Sea, 22°54'N, 68°06'E, depth 16 m.

Temera hardwickii: **BMNH** 1953.8.10.9-10, female, 139 mm TL, 73 mm DW, and adult male, 108 mm TL, 55 mm DW, from Penang, Malaysia, ***syntypes*** of *Temera hardwickii* Gray, 1831. **CAS** 58369, adolescent males, 74 and 84 mm TL, 44 and 49 mm DW, female, 108 mm TL, 59 mm DW, *Anton Bruun* Sta. 0248, 9°54'N, 97°42'E, Andaman Sea, SSW of Kawthaung, Isthmus of Kraa, Burma, 0-200 m. **KUMF** 0014, female, 136 mm TL, 86 mm DW, 19650823, Phuket (Puket), Thailand, depth 91-105 m. **KUMF** 2916, females, 78 and 142 mm TL, 36 and 85 mm DW, adult or late adolescent male, 88 mm TL, 44 mm DW Songkhla Research Vessel, S. Mongkolprasit, 198412, Thailand. **NMS** 2090, adult female, 148 mm TL, 76 mm DW, M. Tweedie, identified by A.W.C.T. Herre, 1940, fish market, Singapore. **NMS** 2110, adult (?) female, 140 mm TL, 81 mm DW, R.L. Chermin, 1954, det. E.R. Alfred, 680615, Changi, Singapore. **SU** 35728, adolescent male, 104 mm TL, 64 mm DW, A.W.C.T. Herre, 1936-1937, Telok Kurau, Perak, Malaysia, **SU** 35736, immature female, 74 mmTL, 38 mm DW, adolescent female, 105 mm TL, 62 mm DW, adult female, 119 mm TL, 62 mm DW (cranium dissected), A.W.C.T. Herre, Singapore. **ZRC** no number, adult male, 82 mm TL, 48 mm DW, no locality data or other

information, presumably Singapore, **ZRC** no number, female (possibly adult), 121 mm TL, 72 mm DW, Ahmad Draman, 19630811, Ponggol, Singapore. **ZRC** 10588, adult male, 109 mm TL, 66 mm DW adult male, Ahmad Draman, 19640801, Ponggol, Singapore. **ZRC** 38918, adult female, 122 mm TL, 78 mm DW, K. Lim, P.K.L. Ng, et al., June 1995, Pulau Bintan, north coast, Tanjung Tondang, Sumatra, Indonesia.

Typhlonarke aysoni: **LJVC** 0424, adult male, 205 mm TL, 110 mm DW, Kaikoura coast, South Island, New Zealand, 110 m. **SIO** 61-149-6A, immature female, 92 mm TL, 48 mm DW, 19610129, NW of Mernoo Bank, South Island, New Zealand, 43°39.0'S, 175°15.0'E, 0-119 m.

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Table 1. Morphometric abbreviations and definitions for torpedinoids

Code	Description	Code	Description
ANF	anterior nasal flap length, from anterior edge of incurrent apertures to rear end of nasal curtain	IG5	distance between medial ends of fifth gill slits
CDM	dorsal caudal margin, upper caudal fin origin to rear tip of fin	INO	least inter-orbital width between eyeballs
CH	greatest vertical height of caudal fin	INS	least width between spiracles
CLB	width across base of clasper	INW	inter-narial width, least distance between excurrent narial apertures
CLI	clasper medial length from anterior end of vent	IOW	inter-narial outer width, nasal curtain base width at incurrent apertures
CLO	clasper length, from pelvic fin base to clasper tip	MOL	mouth length, mid upper lip to line joining corners
COH	height of exposed cornea	MOW	mouth width, distance between mouth corners
COL	anterior – posterior length of exposed cornea	NOW	nostril width from lateral edge of incurrent aperture to medial edge of excurrent aperture
CPH	peduncle height at upper caudal fin origin	PCS	pelvic fin insertion to ventral origin of caudal fin
CPW	caudal peduncle width at upper caudal origin	PDI	least distance between verticals at pelvic fin insertion and first dorsal fin insertion
CVM	ventral caudal fin margin, from ventral fin origin to rear tip	PDO	pelvic fin origins to first dorsal fin origin
DCS	dorsal caudal space, D2 insertion to upper caudal fin origin	PD1	pre-D1, snout tip to first dorsal fin origin
DL	disc length, snout tip to line at rear tips of disc	PD2	pre-D2, snout tip to second dorsal fin origin
DT	greatest thickness at middle of disc	PGL	prebranchial length, snout tip to level of first gill slits
DW	greatest transverse width across disc	PGW	snout tip to level of greatest disc width
D1A	D1 anterior margin from origin to fin apex	PIW	body width at pectoral fin insertions
D1B	first dorsal fin base, from origin to insertion	POB	pre-orbital, snout tip to line at front edge of eyes
D1H	D1 height, vertical distance from fin base to apex	POR	pre-oral length, snout tip to front edge of mouth
D1I	D1 inner margin, from insertion to rear edge	PP2	pre-pelvic length, snout tip to level of pelvic fin origins
D1L	D1 length, from origin to rear edge of fin	PRC	pre-caudal length, from snout tip to dorsal caudal fin origin
D1P	D1 posterior margin from apex to free rear tip	PRN	pre-narial length, midline snout tip to level of nostrils
D2A	D2 anterior margin from origin to fin apex	PSP	pre-spiracular length, snout tip to level of spiracles
D2B	length D2 base, from origin to insertion	P1I	pectoral disc insertion to free rear tip
D2H	D2 height, vertical distance from base to apex	P2A	pelvic fin anterior margin from fin origin to apex
D2I	D2 inner margin from insertion to rear edge of fin	P2B	pelvic fin base from pelvic fin origin to insertion
D2L	D2 length, from origin to rear edge of fin	P2H	pelvic fin height, perpendicular distance from base to apex of fin
D2P	D2 posterior margin, from apex to free rear tip	P2I	pelvic fin inner margin, pelvic fin insertion to rear tip
ESL	distance from rear edge of eyeball to spiracle	P2L	pelvic fin length, from pelvic fin origin to rear tip
EH	height of protruding eyeball	P2P	pelvic fin postero-lateral margin, fin apex to rear tip
EL	anterior-posterior length of protruding eyeball	P2S	pelvic fin span, distance between pelvic fin apices
GS1	width from medial to lateral ends of first gill slit	SPL	anterior-posterior length (diameter) of spiracle
GS2	width of second gill slit	SPW	lateral-medial width (diameter) of spiracle
GS3	width of third gill slit	SVL	snout tip to anterior end of vent
GS4	width of fourth gill slit	TBH	tail base vertical thickness at pelvic fin insertions
GS5	width of fifth gill slit	TBW	tail base width at pelvic fin insertions
HL	head length, tip of snout to level of fifth gill slits	TL	total length, from snout tip to rear end of caudal fin
IDS	interdorsal distance, D1 insertion to D2 origin	VNL	anterior-posterior length of vent (cloaca)
IG1	distance between medial ends of first gill slits		

Table 2. Measurements in mm and proportions as %TL for type specimens of *Electrolux addisoni*. Abbreviations for measurements are defined in Table 1.

	Holotype		Paratype			Holotype		Paratype	
TL	515 mm	%TL	502 mm	%TL		mm	%TL	mm	%TL
PRC	425	83	410	82	GS3	10	1.9	9	1.8
DW	305	59	291	58	GS4	10	1.9	9	1.8
DL	264	51	255	51	GS5	5	1.0	7	1.4
DT	46	8.9	53	11	IG1	50	9.7	51	10
PRN	37	7.2	41	8.2	IG5	34	6.6	27	5.4
POR	32	6.2	42	8.4	VNL	24	4.7	22	4.4
POB	42	8.2	32	6.4	PIW	99	19	80	16
PSP	46	8.9	40	8.0	TBH	32	6.2	36	7.2
PGL	79	15	71	14	TBW	62	12	55	11
HL	132	26	127	25	CPH	15	2.9	15	3.0
PGW	137	27	129	26	CPW	13	2.5	16	3.2
PP2	194	38	186	37	P1I	25	4.9	27	5.4
SVL	225	44	221	44	P2L	123	24	126	25
PD1	300	58	282	56	P2A	81	16	82	16
PD2	369	72	357	71	P2B	82	16	81	16
IDS	33	6.4	27	5.4	P2H	63	12	68	14
DCS	21	4.1	22	4.4	P2I	48	9.3	51	10
PCS	144	28	142	28	P2P	116	23	116	23
PDO	132	26	62	12	P2S	202	39	197	39
PDI	64	12	58	12	CLO	22	4.3	24	4.8
COL	9	1.7	9	1.8	CLI	102	20	95	19
COH	5	1.0	5	1.0	CLB	9	1.7	10	2.0
EL	11	2.1	12	2.4	D1A	75	15	76	15
EH	10	1.9	8	1.6	D1B	31	6.0	36	7.2
INO	24	4.7	24	4.8	D1H	56	11	57	11
NOW	12	2.3	12	2.4	D1I	16	3.1	18	3.6
INW	6	1.2	5	1.0	D1L	52	10	53	11
IOW	18	3.5	16	3.2	D1P	44	8.5	39	7.8
ANF	17	3.3	15	3.0	D2A	73	14	75	15
SPL	14	2.7	13	2.6	D2B	30	5.8	31	6.2
SPW	13	2.5	12	2.4	D2H	48	9.3	46	9.2
INS	17	3.3	17	3.4	D2I	21	4	23	4.6
ESL	0	0.0	0	0.0	D2L	46	8.9	43	8.6
MOL	3	0.6	5	1.0	D2P	35	6.8	37	7.4
MOW	22	4.3	20	4.0	CDM	81	16	80	16
GS1	12	2.3	9	1.8	CVM	58	11	66	13
GS2	10	1.9	9	1.8	CH	63	12	56	11

Table 3. Torpedinoid family-group taxa assigned to the two superfamilies of Compagno (1973), and sorted into currently recognized families.

Superfamily Narcinoidea (Narcinidae + Narkidae) Compagno 1973		
Taxon	**Original Family**	**Current Family**
Tribe (group) Astrapae Gill, 1862	Narcaciontoidae	Narkidae
Tribe (group) Discopygae Gill, 1862	Narcaciontoidae	Narcinidae
Subfamily Discopyginae Gill, 1895	Narcobatidae	Narcinidae
Tribe (group) Narcinae Gill, 1862	Narcaciontoidae	Narcinidae
Family Narcinidae Compagno, 1973		Narcinidae
Subfamily Narcininae Gill, 1862	Narcaciontoidae	Narcinidae
Subfamily Narcininae Gill, 1893	Torpedinidae	Narcinidae
Family Narkidae Bigelow & Schroeder, 1953		Narkidae
Family Narkidae Compagno, 1973		Narkidae
Subfamily Narkinae Fowler, 1934	Torpedinidae	Narkidae
Tribe (group) Temerae Gill, 1862	Narcaciontoidae	Narkidae
Family Temeridae Bigelow & Schroeder, 1953		Narkidae
Subfamily Temerinae Fowler, 1934	Torpedinidae	Narkidae
Superfamily Torpedinoidea (Hypnidae + Torpedinidae) Compagno 1973		
Subfamily Hypninae Gill, 1862	Narcaciontoidae	Hypnidae
Subfamily Hypninae Gill, 1893	Torpedinidae	Hypnidae
Family Hypnidae Compagno, 1973		Hypnidae
Family Narcaciontoidae Gill, 1862		Torpedinidae
Subfamily Narcaciontinae Gill, 1862	Narcaciontoidae	Torpedinidae
Family Narcobatidae Gill, 1895		Torpedinidae
Subfamily Narcobatinae Gill, 1895	Narcobatidae	Torpedinidae
Subfamily Torpedinae Fowler, 1934	Torpedinidae	Torpedinidae
Family Torpedines Müller & Henle, 1841		Torpedinidae
Family Torpedinidae Owen, 1866		Torpedinidae
Family Torpedinidae Bigelow & Schroeder, 1953		Torpedinidae
Family Torpedinidae Compagno, 1973		Torpedinidae
Subfamily Torpedinini Bonaparte, 1838	Rajidae	Torpedinidae
Subfamily Torpedinini Gill, 1893	Torpedinidae	Torpedinidae
Family Torpedinoidae Gill, 1862		Torpedinidae

Table 4. Torpedinoid genera and synonyms. Genus group names that are apparently incorrect subsequent spellings of previously described names are designated by an asterisk (*). Citations for incorrect subsequent spellings are not included in Literature Cited list.

Superfamily Narcinoidea		Superfamily Torpedinoidea	
Genus	**Valid genus**	**Genus**	**Valid genus**
Astrape Müller & Henle, 1837	*Narke*	*Eunarce* Fowler, 1910	*Torpedo*
Bengalichthys Annandale, 1909	*Narke*	*Fimbriotorpedo* Fritsch, 1886	*Torpedo*
Benthobatis Alcock, 1898	*Benthobatis*	*Gymnotorpedo* Fritsch, 1886	*Torpedo*
Crassinarke Takagi, 1951	*Narke*	*Hypnarce* Waite, 1902	*Hypnos*
Cyclonarce Gill, 1862	*Narcine*	*Hypnarea** Sharp, 1903	*Hypnos*
Diplobatis Bigelow & Schroeder, 1948	*Diplobatis*	*Hypos** Cappetta, 1988	*Hypnos*
Discopyge Heckel *in* Tschudi, 1846	*Discopyge*	*Hypnos* Dumeril, 1852	*Hypnos*
Gonionarce Gill, 1862	*Narcine*	*Narcacion* Gill (Klein) 1862	*Torpedo*
Heteronarce Regan, 1921	*Heteronarce*	*Narcobatis** Blainville, 1825	*Torpedo*
*Narcina** Jordan & Seale, 1905	*Narcine*	*Narcobatus* Blainville, 1816	*Torpedo*
Narcine Henle, 1834	*Narcine*	*Notastrape* Whitley, 1932	*Torpedo*
Narcinops Whitley, 1940	*Narcine*	*Tetranarce** Gill, 1895	*Torpedo*
Narke Kaup, 1826	*Narke*	*Tetronarce* Gill, 1862	*Torpedo*
Syrraxis Jourdan *in* Bonaparte, 1835	*Narcine*	*Tetronarcine** Tanaka, 1908	*Torpedo*
Temera Gray, 1831	*Temera*	*Torpedo* Houttuyn, 1764	*Torpedo*
Temerara Tirant, 1929	*Temera*	*Torpedo* Dumeril, 1806	*Torpedo*
Typhlonarke Waite, 1909	*Typhlonarke*		

Table 5. Family Narkidae: species and synonyms, including name changes and one species (*Heteronarce rierai*) originally allocated to the Narcinidae

Nominal species	Valid species
Astrape aysoni Hamilton, 1902	*Typhlonarke aysoni*
Narcine bentuviai Baranes & Randall, 1989	*Heteronarce bentuviai*
Raja capensis Gmelin, 1788	*Narke capensis*
Raja dipterygia Bloch & Schneider, 1801	*Narke dipterygia*
Crassinarke dormitor Takagi, 1951	? = *Narke japonica*
Heteronarce garmani Regan, 1921	*Heteronarce garmani*
Temera hardwickii Gray, 1831	*Temera hardwickii*
Temerara hardwickii Tirant, 1929	*Temera hardwickii*
Bengalichthys impennis Annandale, 1909	*Narke dipterygia*
Torpedo japonica Temminck & Schlegel, 1850	*Narke japonica*
Narcine mollis Lloyd, 1907	*Heteronarce mollis*
Narcine natalensis Fowler, 1925	*Heteronarce garmani*
Heteronarce prabhui Talwar, 1981	*Heteronarce prabhui*
Heteronarce regani von Bonde & Swart, 1924	*Heteronarce garmani*
Heteronarce reirai Lloris & Rucabado, 1991	*Narcine reirai*
Typhlonarke tarakea Phillipps, 1929	? *Typhlonarke tarakea*

Table 6. Vertebral counts of representative narkids. Counts of vertebral centra, and sums of totals and percent vertebral groups. Abbreviations follow text; n = number of specimens.

COUNTS	n	SYN	SYS	SYC	MPN	MPR	MP	DPR	DPN	DP	DC
Electrolux addisoni	2	14 –16	9 --11	5	6 -- 7	23 – 24	30	6 -- 8	54 -- 55	61 -- 62	27 -- 28
Heteronarce	21	10 --14	7 --10	2 -- 5	3 -- 6	15 – 22	19 -- 26	3 -- 10	34 -- 50	34 -- 64	21 -- 29
H. bentuvai	6									57 -- 64	22 -- 25
H. garmani	6	10 --14	7 -- 9	2 -- 5	4 -- 6	15 –20	19 -- 25	8 -- 10	45 --50	45 -- 56	21 -- 29
H. mollis	9	11 –13	7 -- 10	2 -- 4	3 -- 5	16 – 22	21 -- 26	3 -- 7	34 -- 49	34 -- 53	21 --26
Narke	51	8 -- 13	5 -- 10	1 -- 4	2 -- 7	15 – 25	20 -- 29	1 -- 9	19 -- 42	21 -- 51	16 – 28
N. capensis	6	10 --13	7 -- 10	2 -- 4	3 -- 7	21 – 24	26 -- 29	1 -- 4	28 -- 31	31 -- 35	24 -- 28
N. dipterygia	14	8 -- 11	5 -- 9	1 -- 4	2 -- 6	15 –21	20 -- 25	1 -- 5	19 -- 42	21 -- 42	19 -- 25
N. japonica	6	9 -- 12	6 -- 9	2 -- 3	4 -- 5	16 – 25	20 -- 29	5 -- 9	37 -- 42	37 -- 51	16 – 26
N. spp	24	8 -- 11	5 -- 9	1 -- 3	2 -- 5	16 – 25	20 -- 29	2 -- 9	27 -- 42	27 -- 51	17 -- 26
'Crassinarke dormitor'	1	11	9	2	2	16	18	8	38	46	27
Temera hardwickii	7	8 -- 10	5 -- 8	2 -- 3	2 -- 4	20 – 23	24 -- 25	29 --30	24 -- 28	24 -- 30	16 -- 19
Typhlonarke aysoni	2	11 --14	10 --10	1 -- 4	8 -- 8	18 – 24	24 -- 26	3 -- 3	37 -- 48	40 -- 48	22 -- 32
SUMS & RATIOS	**n**	**PCC**	**PC**	**TF**	**TC**	**TS**	**SYN%**	**MP%**	**DP%**	**DC%**	
Electrolux addisoni	2	96 --97	105 -- 108	118 -- 120	123 -- 125	132 -- 136	12 -- 13	25 -- 18	52	23	
Heteronarce	21	63 - 79	71 - 86	84 - 104	81 - 108	95 – 115	10 -- 15	18 -- 31	41 -- 56	22 -- 29	
H. bentuvai	6				81 -- 86						
H. garmani	6	73 --79	82 -- 86	94 -- 104	98 -- 108	106 -- 115	10 -- 15	18 --25	48 -- 56	22 -- 28	
H. mollis	9	63 -- 78	71 -- 86	84 -- 99	87 -- 102	95 -- 111	11 -- 14	21 – 31	41 -- 54	23 -- 29	
Narke	51	48 -- 75	53 -- 82	65 -- 92	69 -- 95	74 -- 102	10 -- 16	22 -- 37	32 -- 57	18 – 32	
N. capensis	6	61 -- 66	70 -- 75	83 -- 88	87 -- 90	96 -- 99	12 -- 16	31 -- 33	36 -- 40	27 -- 32	
N. dipterygia	14	48 -- 63	53 -- 71	65 -- 85	69 -- 86	74 -- 94	10 -- 14	24 -- 35	32 -- 49	256 – 32	
N. japonica	6	66 -- 75	73 -- 82	87 – 92	90 -- 95	97 -- 102	10 -- 14	22 -- 32	40 -- 57	18 – 28	
Narke spp.	24	54 -- 75	61 -- 82	71 -- 92	73 -- 95	79 -- 102	10 -- 13	26 -- 34	37 -- 57	23 -- 40	
'Crassinarke dormitor'	1	66	75	91	93	102	12	20	51	30	
Temera hardwickii	7	51 -- 58	59 -- 63	65 -- 74	67 -- 77	75 -- 82	11	33 -- 39	37 -- 41	24 -- 26	

Table7. Narkid intestine spiral valve counts (number of turns); total lengths in mm.

Species	Specimens	Count
Electrolux addisoni: SAM-36908, adult male, 502 mm		17
Heteronarce garmani: SAM-34813, adult male, 256 mm		9
Heteronarce garmani: SAM-34813, adult male, 289 mm		8
Narke capensis: A12093 +040-1035, adult female, 231 mm		10
Narke capensis: A14742 111 010-2074, adult male, 215 mm		10
Typhlonarke aysoni: LJVC-0424, adult male, 208 mm		10

Table 8. Tooth row counts of narkids; total lengths in mm; upper jaw rows / lower jaw rows.

Species	Specimens and counts
Electrolux addisoni	SAIAB - holotype adult male, 515 mm; 15 / 17
Electrolux addisoni	SAM – paratype, adult male, 502 mm; 16 / 18
Heteronarce bentuvai	HUJ - holotype, adult male, 191 mm; 11 / 11
Heteronarce garmani	SAM-34813, adult male, 256 mm; 11 / 11
Heteronarce garmani	SAM-34813, adult male, 289 mm; 11 / 10
Heteronarce mollis	Lloyd (1907): 10 – 12 / 10 -- 12
Heteronarce prabhuai	Talwar (1981): Types: 10 – 12 / 11 – 12
Narke capensis	A12093 adult female, 231 mm; 16 / 14
Narke dipterygia	SU? adult female, 164 mm; 17 / 21
Typhlonarke aysoni	Garrick (1951): 10 – 12 / 10 – 12
Typhlonarke aysoni	LJVC-0424, adult male, 205 mm; 10 / 11
Typhlonarke aysoni	SIO-61-149-6A, immature female, 92 mm; 8 / 7
Typhlonarke tarakea	Garrick (1951): 11 / 11

Table 9. Measurements of *Heteronarce* spp. in %TL for *H. garmani* and holotypes of *H. bentuvai* (after Baranes & Randall, 1989) and H. prabhui (after Talwar, 1981)

	garmani	*garmani*	*garmani*	*garmani*	*garmani*	*garmani*	*bentuvai*	*prabhui*
	SAM-	SAM-	Benguela	Benguela	Benguela	BMNH-	HUJ	ZSI
	34813	34813	30-98	30-98	30-98	1921.3.1.3	13612	F7614/2
						Holotype	Holotype	Holotype
	Adult	Adult	Adolescent	Juvenile	Immature	Adolescent	Adult	Adult
	male	male	male	female	female	male	male	male
TL	256	289	145	132	127	164	191	220
PRC	82	80	83	80	84	85	79	79
DW	48	43	48	52	51	42	48	51
DL	47	45	50	49	50	49	48	49
DT	13	12	13	12	12	9.8		
PRN	10	10	9.9	8.0	11	12	3.7	
POR	12	12	12	10	13	10	7.3	11
POB	9.4	11	13	10	13	13	8.4	11
PSP	12	13	15	13	15	19	13	
PGI	17	17	18	18	19	30	16	
HL	29	28	31	31	31	24	26	
PGW	31	32	36	37	35	43		
PP2	44	41	42	43	43	49		
SVL	47	47	49	51	50	45	49	46
PD1	61	61	63	63	64		58	57
PD2	71	70	72	70	72	74	71	67
IDS	4.4	4.4	3.1	2.4	1.6	5.8	4.7	4.8
DCS	3.4	2.0	4.2	2.7	2.4	5.5	3.7	
PCS	23	24	23	15	15	27		
PDO	21	19	20	18	19	23		
PDI	11	9.6	9.7	5.5	6.3	11		
COL	1.7	1.6	2.0	1.8	1.9	1.2		
COH	1.0	0.6	1.0	1.0	0.2	0.6		
EL	3.2	2.7	3.1	4.2	3.6	1.8	2.6	
EH	3.0	2.1	2.4	2.0	1.9	1.2		
INO	5.1	5.5	4.7	6.3	6.3	7.9	8.9	
NOW	1.8	1.3	1.4	2.3	2.0	2.1		
lNW	1.2	0.9	1.6	1.2	1.6	0.6		
IOW		3.3	3.6	3.8	3.1	3.4	5.2	
ANF	3.4	2.8	2.9	2.2	2.4	1.8	3.7	
SPL	1.3	1.7	1.4	1.0	1.3	1.2	2.1	
SPW	1.7	1.7	1.5	1.4	0.9	1.2		
INS	6.5	6.9	6.4	7.0	7.9	6.7	6.8	6.1
ESL	0.4	0.3	0.3	0.7	0.0	0.3	1.0	
MOL	0.0	0.3	0.0	0.0	0.0	1.2		
MOW	3.0	2.9	3.4	3.5	1.8	4.3	5.2	4.8
GS1	1.5	1.0	1.6	1.2	1.3	1.2		

Table 9 continued

GS1	1.5	1.0	1.6	1.2	1.3	1.2		
GS2	1.1	1.1	1.3	1.4	1.3	1.8		
GS3	1.3	1.1	1.5	1.4	1.2	1.8		
GS4	1.3	1.2	1.7	1.3	1.1	1.8		
GS5	1.4	1.1	1.6	1.3	0.9	1.2		
IG1	10	9.3	12	11	12	12	13	15
IG5	6.4	6.2	6.4	6.4	6.3	7.3	8.9	8.2
VNL	5.6	3.3	3.4	4.5	3.9	4.9		
PIW	20	17	20	24	22			
TBH	5.3	5.8	6.2	6.7	5.5	6.7		
TBW	11	9.9	12	13	11	11		
CPH	3.4	3.0	3.0	2.5	2.4	3.0		
CPW	4.0	3.8	4.3	4.1	4.7	3.0		
P1I	43	41	43	47	0.0	41		
P2L	5.2	2.7	5.9	6.1	0.0	0.0		
P2A	22	21	21	24	24	20		
P2B	13	14	12	11	11	11	11	
P2H	16	17	17	20	21	15		
P2I	9.7	9.2	9.6	10	15	9.1		
P2P	6.2	4.7	6.9	6.1	3.9	4.0	1.6	
P2S	16	15	16	17	17	14	19	
CLO	34	30	35	33	33	28		
CLI	5.2	4.2	3.0			5.5	11	
CLB	20	21	15			15		
D1L	2.5	2.4	2.1			2.4		
D1A	7.6	8.6	8.5	7.8	10	7.9		
D1B	9.3	12	9.1	10	11	9.5	9.4	
D1H	5.3	6.3	5.2	5.1	5.8	5.5	7.3	5.7
D1I	6.6	5.7	4.0	6.1	5.5	5.5	6.8	
D1P	2.3	2.6	2.7	2.4	1.6	3.4		
D2L	4.9	3.9	4.2	5.2	3.9	4.9		
D2A	7.7	9.4	8.3	9.2	8.7	8.5		
D2B	11	13	10	12	11	11	6.8	
D2H	6.1	6.9	5.5	6.3	5.5	4.9	3.1	5.7
D2I	7.1	5.6	4.9	6.2	6.3	4.3	1.6	
D2P	1.8	2.4	2.0	2.4	1.6	5.5		
CDM	5.0	4.2	4.6	4.9	4.7	4.6		
CVM	17	18	17	17	16	15	24	
CH	12	14	13	13	13	13	18	

LITERATURE CITED

ANNANDALE, N. 1909. Report on the fishes taken by the Bengal fisheries steamer "Golden Crown". Part I. - Batoidei. *Memoirs of the Indian Museum*, **2**(1): 1-60.

BARANES, A., & J.E. RAMDALL. 1989. *Narcine bentuviai*, a new torpedinoid ray from the northern Red Sea. *Israel Journal of Zoology*, **36**: 85-101, pl. 1, fig. 1-9.

BIGELOW, H.B., & W.C. SCHROEDER. 1953. Chapter one, Sawfishes, Guitarfishes, Skates and Rays. *In* Fishes of the Western North Atlantic. Memoirs of the Sears Foundation for Marine Research (1) **2**: 1-514.

BONAPARTE, C.L. 1838. Selachorum tabula analytica. Nuovi Annali delle Scienze Naturali, Bologna, series 1, **2**: 195-214.

CARROLL, R.L. 1988. Vertebrate paleontology and evolution. W.H. Freeman, New York, pp. i-iv, 1-698.

COMPAGNO, L.J.V. 1973. Interrelationships of living elasmobranchs. *In* P. H. Greenwood, R. S. Miles and C. Patterson (editors), Interrelationships of fishes. *Zoological Journal of the Linnaean Society*, London, Supplement 1, **53**: 15-61.

COMPAGNO, L.J.V. 1977. Phyletic relationships of living sharks and rays. *American Zoologist*, **17**(2): 303-322

COMPAGNO, L.J.V. 1984. FAO Species Catalogue. Vol. 4, Sharks of the World. An annotated and illustrated catalogue of shark species known to date. *FAO Fisheries Synopsis No. 125*, **4**(1): i-viii, 1-250, **4**(2): i-x, 251-655.

COMPAGNO, L.J.V. 1986. Family Narkidae, *in* M.M.Smith & P.C. Heemstra, *eds. Smith's Sea Fishes, 1st edition, first impression*. Macmillan South Africa Publishers, Johannesburg, South Africa, 113-114.

COMPAGNO, L.J.V. 1988. *Sharks of the Order Carcharhiniformes*. Princeton University Press, Princeton, New Jersey, pp. i-xxii, 1-572. Reprinted by Blackburn Press, 2003, pp. i-xxii, 1-572, with new forward.

COMPAGNO, L.J.V. 1990. Evolution and diversity of sharks. *In* S. H. Gruber, *ed.*, Discovering sharks. A volume honoring the work of Stewart Springer. Underwater Naturalist, Bulletin of the American Littoral Society, **19-20**(4/1): 15-22, figs

COMPAGNO, L.J.V. 1995. Additions to and revisions of Family Narkidae and Narcinidae, *in* M.M.Smith & P.C. Heemstra, *eds. Smith's Sea Fishes, 1st edition, third impression (revised)*. Southern Book Publishers, Johannesburg, South Africa, vi-vii.

COMPAGNO, L.J.V. 1999a. Chapter 1. Systematics and body form. Chapter 3. Endoskeleton. Appendix. Checklist of living elasmobranchs. *In* W. C. Hamlett, *ed.. Sharks, skates and rays. The biology of elasmobranch fishes*. Johns Hopkins Press, pp. 1-42, 69-92, 471 to 498, figs. 1.1-1.15, 3.1-3.8.

COMPAGNO, L.J.V. 1999b. An overview of chondrichthyan systematics and biodiversity in southern Africa. *Transactions of the Royal Society of South Africa*, 1999 **54**(1): 75-120, fig. 1-9, tab. 1-2.

COMPAGNO, L.J.V. 2001, Sharks of the World. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). An annotated and illustrated catalogue of the shark species known to date. FAO Species Catalogue for Fisheries Purposes (1): i-v, 1-269, figs. 1-163, 160 maps.

COMPAGNO, L. J. V. 2005. Chapter 16. Checklist of living Chondrichthyes. *In* W. C. Hamlett, *ed., Reproductive biology and phylogeny of Chondrichthyes*. Enfield, New Hampshire, USA, Science Publishers, Inc.: 503-548.

COMPAGNO, L.J.V., M. DANDO & S. FOWLER. 2005. *A Field Guide to the Sharks of the World*. First printing, first impression. Harper-Collins, London. Pp i-vii, 9-368, monochrome figs. 1-60, color pls. 1-64.

COMPAGNO, L.J.V., D.A. EBERT & M.J. SMALE. 1989. *Guide to the sharks and rays of southern Africa*. Struik Publishers, Cape Town, 160 pp.

COMPAGNO, L.J.V., & P.R. LAST. 1999a. Order Torpediniformes. Narkidae. Sleeper rays. In Carpenter, K.E. and V.H. Niem *(eds)*, 1999. *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific*. Rome, FAO, 3: 1443-1446, figs.

COMPAGNO, L.J.V., & P.R. LAST. 1999b. Order Torpediniformes. Hypnidae. Coffin rays. In Carpenter, K.E. and V.H. Niem (eds), 1999. *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific*. Rome, FAO, 3: 1447-1448.

COMPAGNO, L.J.V., & P.R. LAST. 1999c. Order Torpediniformes. Torpedinidae. Torpedos. In Carpenter, K.E. and V.H. Niem (eds), 1999. FAO species identification guide for fishery purposes. *The living marine resources of the Western Central Pacific*. Rome, FAO, 3: 1449-1451,

COMPAGNO, L.J.V., P.R. LAST, B. SERET, & M. DE CARVALHO. 1999. Batoid Fishes. In Carpenter, K.E. and V.H. Niem (*eds*), 1999. *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific*. Rome, FAO, 3: 1398-1409, figs.

COMPAGNO, L.J.V., & T.R. ROBERTS. 1982. Freshwater stingrays (Dasyatidae) of Southeast Asia and New Guinea, with description of a new species of *Himantura* and reports of unidentified species. *Environmental Biology of Fishes*, **7**(4): 321-339.

COMPAGNO, L.J.V., & T.R. ROBERTS. 1984. Marine and freshwater stingrays (Dasyatidae) of West Africa, with description of a new species. *Proceedings of the California Academy of Sciences*, series 4, **43**: 283-300, fig. 1-10.

DE CARVALHO, M.R. 1999. *A systematic revision of the electric ray genus Narcine Henle, 1834 (Chondrichthyes, Torpediniformes: Narcinidae), and the higher level-phylogenic relationships of the orders of elasmobranch fishes (Chondrichthyes)*. Unpublished Ph.D. Thesis, City University of New York, pp. i-xxxii, 1-704, fig. 1-116.

DE CARVALHO, M.R., L.J.V. COMPAGNO, & P.R. LAST. 1999. Order Torpediniformes. Narcinidae. Numbfishes. *In* Carpenter, K.E. and V.H. Niem (*eds*), 1999. *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific*. Rome, FAO, **3**: 1433-1442, figs.

DE CARVALHO, M.R., B. SERET, & L.J.V. COMPAGNO. 2002. A new species of electric ray of the genus *Narcine* Henle, 1834 from the southwestern Indian Ocean (Chondrichthyes: Torpediniformes: Narcinidae). *South African Journal of Marine Science*, **24**: 135-149, figs. 1-7, tab. 1.

EBERT, D.A. 1990. *The taxonomy, biogeography and biology of cow and frilled sharks (Chondrichthyes: Hexanchiformes)*. Unpub. Ph.D. thesis, Rhodes University, Grahamstown, 308 pp.

ESCHMEYER, WILLIAM N. 1990. *Catalog of the genera of Recent fishes*. California Academy of Sciences, San Francisco, 697 pp.

ESCHMEYER, WILLIAM N. 1998. *Catalog of fishes*. Vol. 1, Introductory materials. Species of fishes (A-L): 1-958. Vol.

2. Species of fishes (M-Z): 959-1820. Vol. 3. Genera of Fishes. Species and genera in a classification. Literature Cited. Appendices: 1821-2905. Also CD-ROM with Access database.

FOWLER, H. W. 1925a. Descriptions of three new marine fishes from the Natal coast. *Annals of the Natal Museum*, **5**(2): 195-200. fig. 1-3.

FOWLER, H. W. 1925b. Fishes from Natal, Zululand and Portuguese East Africa. *Proceedings of the Academy of Natural Sciences, Philadelphia*, 1925, **77**: 187-268, fig. 1-4.

FOWLER, H. W. 1934. Descriptions of new fishes obtained 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *Proceedings of the Academy of Natural Sciences, Philadelphia*, **85**: 233-367

FOWLER, H.W. 1941. The fishes of the groups Elasmobranchii, Holocephali, Isospondyli, and Ostariophysi obtained by United States Bureau of Fisheries Steamer Albatross in 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *Bulletin of the United States National Museum* (100) **13**: 1-879.

FOWLER, H. W. 1970. A catalog of world fishes (XII). *Quarterly Journal of the Taiwan Museum* **23**(1-2): 39-126.

GARMAN, SAMUEL. 1913. The Plagiostoma. *Memoirs of the Museum of Comparative Zoology, Harvard*, **36**: 1-515.

GARRICK, J. A. F. 1951. The blind electric rays of the genus *Typhlonarke* (Torpedinidae). *Zoological Publications, Victoria University College*, (15): 1-6.

GILL, T. 1862. Analytical synopsis of the Order of Squali; and revision of the nomenclature of the genera. Squalorum generum novorum descriptiones diagnosticae. *Annals of the Lyceum of Natural History of New York*, 7: 367-413.

GILL, T. 1893. Families and subfamilies of fishes. *Memoirs of the National Academy of Sciences, United States of America*, **6**(6): 125-138.

GILL, T. 1895. Notes on the synonymy of the Torpedinidae or Narcobatidae. *Proceedings of the United States National Museum*, **18**(1050): 161-165.

HASWELL, W.A. 1885. Studies on the elasmobranch skeleton. *Proceedings of the Linnaean Society of New South Wales*, **9**: 71-119.

HENLE, F. G. J. 1834. *Ueber* Narcine, *eine neue Gattung electrischer Rochen nebst einer synopsis der electrischer Rochen*. Königlichen anatomischen Museum, Berlin, 1, pp. 1-44, pls. 1-4.

HOLMGREN, N. 1941. Studies on the head in fishes. Embryological, morphological, and phylogenetical researches. Part II. Comparative anatomy of the adult selachian skull, with remarks on the dorsal fins in sharks. *Acta Zoologica*, **22**: 1-100. figs. 1-74.

HUMAN, B. A. 2006. A taxonomic revision of the catshark genus *Holohalaelurus* Fowler 1934 (Chondrichthyes: Carcharhiniformes: Scyliorhinidae), with descriptions of two new species. *Zootaxa* (1315): 1-56, figs. 1-17, figs. 1-5, append. 1.

IUCN. 2006. International Union for the Conservation of Nature, Species Survival Commission. Red List web site at http://www.iucnredlist.org

KOORHNHOF, A. 1995. *The dive sites of South Africa. Comprehensive coverage of diving and snorkeling*. New Holland Publishers, London, Cape Town, Sydney, Singapore, 1-183.

LAST, P.R., & J.D. STEVENS. 1994. *Sharks and rays of Australia*. CSIRO, Australia, pp. i-ix, 1-513, 1400 black and white ill., color pls. 1-84.

LEIGH-SHARPE, W. H. 1922. The comparative morphology of the secondary sexual characters of Holocephali and elasmobranch fishes. Memoir IV. *Journal of Morphology* **36**: 199-220.

LEIGH-SHARPE, W. H. 1924. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Memoir VI. *Journal of Morphology* **39**: 553-566.

LEIGH-SHARPE, W. H. 1926. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Memoir VIII. *Journal of Morphology* **42**: 307-320.

LINDBERG, G. U. 1971 (1974). *Fishes of the world. A key to families and a checklist*. Pp. 1-545, fig. 1-986. Translated by Israel Program for Scientific Translations, 1974. Halsted Press, New York.

LLORIS, D. & J.A. RUCABADO. 1991. *Heteronarce rierai*, a new narkid ray from Mozambique, Western Indian Ocean. *Japanese Journal of Ichthyology*, **37**(4): 327-332, fig. 1-3.

LLOYD, R. E. 1907. Contributions to the fauna of the Arabian Sea, with descriptions of new fishes and crustacea. *Records of the Indian Museum*, **1**(1): 1-12.

LLOYD, R. E. 1909. A description of the deep sea fish caught by the R.I.M.S. Ship *Investigator* since the year 1900, with supposed evidence of mutation in *Malthopsis*. *Memoirs of the Indian Museum*, 2(3): 139-180.

MCEACHRAN, J.D., & L.J.V. COMPAGNO. 1982. Class Chondrichthyes. In S. Parker, ed. *Synopsis and classification of living organisms*. McGraw-Hill, **2**: 831-858, figs, 1113-1114.

MCEACHRAN, J.D., K.A. DUNN, & T. MIYAKE. 1996. Interrelationships of the batoid fishes (Chondrichthyes: Batoidei). *In* M.L.J. Stiassny, L.R. Parenti, & G.D. Johnson, Eds, *Interrelationships of fishes*. Academic Press, San Diego, London, 63-84, fig. 1-13.

MCKAY, R.J. 1966. Studies on western Australian sharks and rays of the families *Scyliorhinidae, Urolophidae*, and *Torpedinidae*. *Journal of the Royal Society of Western Australia*. **49**(3): 65-82.

MÜLLER, J. & F. G. J. HENLE. 1841. *Systematische Beschreibung der Plagiostomen*, (part 3) pp. 103-200. Veit, Berlin.

NELSON, J. S. 1976. Fishes of the world. Pp. i-ix, 1-416. Wiley-Interscience, New York.

NELSON, J. S. 1984. Fishes of the world, second edition. Pp. i-xv, 1-523. Wiley-Interscience, New York.

NELSON, J. S. 1994. Fishes of the world, third edition. Pp. i-xvi, 1-600. John Wiley & Sons, Inc., New York.

RASS, T. S., & G. U. LINDBERG. 1971. Modern concepts of the classification of living fishes. *Journal of Ichthyology* **11**: 302-319 (translated by the American Fisheries Society).

REGAN, C. T. 1921. New fishes from deep water off the coast of Natal. Annals and Magazine of Natural History, series 9, **7**(41): 412-420.

SHIRAI, S. 1996. Phylogenetic interrelelationships of neoselachians (Chondrichthyes, Euselachii). *In* M.L.J. Stiassny, L.R. Parenti, & G. D. Johnson, *Eds, Interrelationships of fishes*. Academic Press, San Diego, London, 9-34, fig. 1-4.

SMITH, H. M. 1912. The squaloid sharks of the Philippine Archipelago, with descriptions of new genera and species. *Proceedings of the United States National Museum*, **41**(1877): 677-685, figs. 1-4, pls. 50-54.

TALWAR, P. K. 1981. The electric rays of the genus *Heteronarce* Regan (Rajiformes; Torpedinidae), with the description of a new species. *Bulletin of the Zoological Survey of India*, **3**(3): 147-151, fig. 1.

VON BONDE, C., & D. B. SWART. 1923. The platosomia (skates and rays) collected by the S. S. "Pickle". *Union of South Africa, Fisheries Marine Biological Survey, Report (3), 1922*, special Report (5), pp. 1-22 pls. 20-23.

WALLACE, J.H. 1967. The batoid fishes of the east coast of southern Africa. Part III: Skates and electric rays. *South African Association for Marine Biological Research, Oceanographic Research Institute, Investigational Report* (17): 1-62, fig. 1-29.

WHITLEY, G. P. 1940. *The fishes of Australia. Part I. The sharks, rays, devilfish, and other primitive fishes of Australia and New Zealand*. Australian Zoology Handbook, pp. 1-280. Royal Zoological Society of New South Wales, Sydney.

ZHU YUANDING & MENG QUINGWEN. 1979. A study of the lateral-line canals system and that of Lorenzini ampullae and tubules of Chondrichthyes fishes of China. *Monographs of Fishes of China*, Science and Technology Press, Shanghai, i-iv, 1-132, figs. 1-71.

Fishes of the genus *Helcogramma* (Blennioidei: Tripterygiidae) in the Western Indian Ocean, including Sri Lanka, with descriptions of four new species.

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Abstract. Fifteen species of the tripterygiid fish genus *Helcogramma* are recognised from the Western Indian Ocean (including Sri Lanka and the southeastern coast of India). *Helcogramma shinglensis* Lal Mohan is recognised as a valid species and four species are described as new: *Helcogramma alkamr*, which is similar to *H. chica* Rosenblatt, is known from the Comoro Islands, the Seychelles and Mauritius; *Helcogramma serendip*, apparently confined to Sri Lanka and possibly a sibling species to *H. alkamr; Helcogramma ememes* from the Seychelles and the East African coast, which is similar to *H. hudsoni* Schultz, and *Helcogramma rharhabe*, one of the *H. obtusirostre* complex of species, and which appears confined to the east coast of Africa from northern Mozambique to East London. Diagnoses of the other Western Indian Ocean species and a key are provided.

Keywords: taxonomy, Tripterygiidae, *Helcogramma*, new species, Western Indian Ocean

INTRODUCTION

The genus *Helcogramma* McCulloch & Waite 1918 has been revised only once, by Hansen, in 1986. Subsequent studies on tripterygiid fishes have been regional (e.g. Fricke 1994 & 1997), have described new species (e.g. Fricke & Randall 1992; Randall & Clark 1993), or dealt specifically with the *Helcogramma fuscopinna* complex (Williams & McCormick 1990; Williams & Howe 2003). Hansen recognised 12 species, describing four as new. She also synonymised many nominal species, several as *Helcogramma obtusirostre* (originally described by Klunzinger from the Red Sea), a species which she considered to occur widely in the Indo-West Pacific Ocean. Williams and McCormick (1990) recognised that *H. fuscopinna* is a complex of at least eight species. Fricke (1994, 1997) described a further three new species for the genus. This study recognises 15 species from the Western Indian Ocean of which four are described as new, bringing the total number of species in *Helcogramma* to some 35.

Notwithstanding Fricke's record of variations of 4, 5 or even 6 in counts of fin spines or rays in a single species, this review shows little morphometric variation in *Helcogramma* species. At most, fin elements will vary by 3, and then the number of counts off the norm (mode) are generally very low. Lateral-line scale counts do show greater variation in some species. This study also shows that several species have fin-element counts that do not separate them from each other. It was this factor, I believe, that encouraged Hansen to synonymise a number of species as *Helcogramma obtusirostre*. However, individuals from different areas can be separated on the basis of colour pattern (see e.g. Williams & Howe 2003; Holleman 2006). In the Western Indian Ocean there are three species that can be ascribed to the *Helcogramma obtusirostre* complex. There are additional species in the Western Pacific Ocean-as well as one in the Southern Atlantic-that can also be ascribed to this complex.

METHODS

All measurements were made with pin dial calipers under a binocular microscope and are given in millimeters to a single decimal place. Ratios are calculated as the number of times a given measured length is contained in either the standard length or the head length. The measurement of head profiles, as measured in Holleman (1982), are fairly 'crude', but serve to indicate differences in skull structure. All counts were made under a microscope, including vertebrae, which were counted from radiographs. Pectoral-fin ray and lateral-line counts were made on the left side. Specimens on rare occasion have lost or gained a single ray in one of the pectoral fins. If the count was not as expected, the right side was counted, and if "normal", recorded; if not, the "non-normal" count was recorded. The counts are given, from the dorsalmost fin ray, as number of undivided rays, number of divided rays, number of undivided rays, e.g. 2, 7, 7. The numbers of divided and undivided rays were found to be remarkably consistent for most species.

Body scales of tripterygiid fishes are deciduous and often missing. If the last lateral-line scale on the left side was not followed by an ordinary body scale, the right side's scales were counted. If neither side was complete, the count was not recorded. Most species of *Helcogramma* have a naked area laterally along the base of the first and often the second dorsal fins. In species in which the body scales do not extend to the base of these fins, the scales decrease in size and become very thin as they approach the fin bases. They are best seen

Table 1. Selected characters of WIO species of *Helcogramma*; usual/modal counts are given in parenthesis.

Species	Second & third dorsal fins	Anal fin	Pectoral fins	Lateral line	Total lateral scales	Mandibular pores	Vertebrae	Nape	Ht. D1 cf D2
alkamr WIO islands n = 174	XIII–XIV + 10–11	19– 20	16: 1, 8, 7	19–25 (mode 21) few with 19 or 23–24	36–39 (37–38)	5 + 1 + 5 (⅔) 6 + 1 + 6 (⅓)	10 + 25–26	naked	<½
billi Sri Lanka n = 5	1XIII–XIV + 10–11 (XIII + 10)	17–20 (19)	16: 2, 7, 7	27–33 (mode 30)	38–39	2–3 + 1 + 2–3	10 + 25–26	scaled	>½ ♂ <½ ♀
elliotti SE India n = 6	XIII + 9–10 (XIII + 9)	18–19 rarely 20	16: 1, 8, 7	33–37† (34–35)	36–38 (38)	5–7 + 3–5 + 5–7	10 + 24–25	naked	= ♂ < ♀
ememes E. Africa, Seychelles n = 83	XII –XIV + 9–11	18–20 (19)	15: 1, 7, 7 or 1, 8, 6 or 2, 7, 6	19–23 (21)	36–38 (37)	4–7 + 3 + 4–7 (rarely 7)	10 + 24–27 (26)	naked	~ ½
fuscopinna WIO n = 137	XIII–XV + 10–12 (XIV + 11)	19–22 (21)	17: 1, 9, 7 seldom 16	22–30	38–40 (39–40)	5–8 + 1–2 + 5–8 (rarely 8)	10 + 27 rarely 26–28	naked	= ♂ < ♀
**larvata* Maldives n = 1	XI–XII + 8–9 (XII + 8–9)	16–18	15: 4, 4, 7	20–22	32–35	2–3 + 1 + 2–3	10 + 24–25	naked	½ - ⅔
**maldivensis* Maldives n = 1	XII–XIV + 9–11 (XIII + 10)	18–22 (22)	15: 3, 6, 6	13–21 usually 16–17	36–37	3 + 2 + 3	10 + 25–26	naked	~ ½
microstigma Comores to Inhaca n = 27	XII–XIV + 10–11	18–20 (19–20)	15: 2, 6, 7 or 16: 2, 7, 7	24–31 (27–28)	37–38	4 + 1 + 4 rarely 3 + 1 + 3	11 + 23–25 (24)	partly scaled	> ♂ = ♀
obtusirostre Red Sea and Oman n = 20	XII–XIII + 9–10 rarely XII spines or 9 rays	18–19 (19)	16: 2, 7, 7	20–23 (21–22)	36–38 (37–38)	4 + 1 + 4	10 + 25–26	naked	~ ½
rharhabe East London to Bazaruto n = 236	XII–XIV + 10–11 (XIII + 10)	18–20 rarely 18 or 20	16: 1, 8, 7 sometimes 15	20–31 (mode 24)	37–38 (38)	5 + 1 + 5	10 + 24–25	naked	~ ½
rosea Sri Lanka to Phuket n = 42	XI–XIVI + 10–12 rarely 10	18–20 (20) rarely 18	16: 2, 7, 7	23–29 usually 25–27	36–38 usually 37	3–4 + 1 + 3–4	11 + 24–26 (25)	scaled	> ♂ = ♀
serendip Sri Lanka n = 26	XIII + 10	18–19 (19)	16: 2, 7, 7	20–22 (21)	36–39 (38)	4 + 1 + 4	10 + 25 rarely 26	naked	< ½
shinglensis SE India n = 20	XIII + 10	19–20 (19)	16: 1, 8, 7 sometimes 15	21–24	37–38	4–6 + 3 + 4–6	10 + 24–25	naked	~ ½
steinitzi Red Sea and Oman n = 35	XII–XIV + 10–12 (XIII + 11) (JER 10–12)	**19–21 (20)	16: 2, 7, 7 (both Clark & Randall have 15–17)	21–27	**37–42 R Sea 38–40 Oman	3 + 1–2 + 3	11 + 24–25	scaled	= ♂ < ♀
striata Sri Lanka and east n = 57	XIII–XV + 10–12 (XIII or XIV + 11- see Table 7)	†19–23 (20–22) (WIO 19–20)	16: 3, 6, 7 or 2, 7, 7 usually	†14–20 (WIO 17–18)	38–39 (39)	3 + 2 + 3	10 + 25–27	scaled	~½

* Counts from Fricke & Randall, 1992
** Counts from Clark, 1979 and J E Randall, 1992
† Counts from Hansen, 1986
n = number of specimens examined in this study

stained with Cyanine Blue (Saruwatari et al. 1997). Nape scales, when present, and only on the side of the nape, are also best seen when stained with Cyanine Blue. Few tripterygiid species have scales in the predorsal midline. It was found that for species which do not have a fully scaled nape, such as *Helcogramma microstigma*, the number of transverse scale rows increases with increasing size of the fish. This means that while scales above the lateral line may not extend to the base of the second dorsal fin in apparently immature (smaller) specimens, they may do so in larger, presumably mature specimens, such as darkly pigmented males. The nape would then be referred to as scaled, and the extent of the scalation noted. Transverse scale counts are not given for the species in this study. Total lateral scales were counted as a continuation of the lateral line to the base of the caudal fin. Tripterygiids have from 0-3 rows of scales of varying size on the base of the caudal fin. These are not included in the count but noted separately.

Williams & McCormick (1990) derived a method of representing dorsal element counts from radiographs which included the number of pterygiophores without a spine between the second and third dorsal fins, 0 being the condition where the first pterygiophore supporting a segmented ray does not support a spine. I do not follow this method, but indicate the number of "free" pterygiophores; i.e. carrying neither a spine nor a segmented ray. This number generally varies between 0 and 2 and is not consistent for a species. The method of counting vertebrae follows Holleman (1982) and is the same as that of Williams & McCormick (1990). They are given as the number of precaudal + the number of caudal vertebrae, and includes the compound terminal centrum (not stated in Holleman, 1982).

Mandibular pore counts follow Hansen (1986), who found that the mandibular pore patterns of *Helcogramma* species were consistent for a species and often diagnostic. They have been found to be so in *Enneapterygius* Rüppell 1835, as well (Holleman, 2006), and they are given as number of pores in left hand canal + number of symphyseal pores + number of pores in right hand canal.

In describing colour patterns the terms "short bar" is used for darkly pigmented (unless otherwise stated) bars that extend from the dorsum to the lateral line or just below. The term "saddle" is used for lightly pigmented areas that are quite clearly defined and often rounded that extend from the dorsum down either side, much like the saddle on a horse's back.

A summary of selected characters and morphometric counts for the species is given in Table 1. The known distributions of the various species is shown in Fig. 1. The map is also marked with the biogeographic boundaries suggested in Santini & Winterbottom (2002), which gives some idea of the distribution of species in relation to different biogeographic areas.

Genus *Helcogramma* McCulloch & Waite

Helcogramma McCulloch & Waite 1918: 51; type species *H. decurrens* McCulloch & Waite 1918, by original designation.

Diagnosis. Small to medium-sized tripterygiid fishes with fusiform bodies, ranging in length from less than 28 mm SL (*Helcogramma chica*) to nearly 50 mm SL (*H. ellioti*). First dorsal fin with 3 spines; anal fin with a single, short spine, usually less than half the length of the first ray. Pelvic fins with one short, hidden spine and two simple, segmented rays, which may be joined by membrane for part of their length.

Mandibular canals with 1 or (rarely) 2 pores at the symphysis, or 3–5 pores arranged symmetrically about the symphysis, and 2–8 on either side along the dentaries. Exposed posterior margin of post-temporal bones with fine serrations.

Body with ctenoid scales; nape naked or scaled; abdomen and pectoral fin-bases always naked. Head always without scales. Lateral line continuous, of 14–35 pored scales, running in a upwardly concave curve from the post-temporal to mid-body and extending to below the second dorsal fin or to the base of the caudal fin. Base of caudal fin with 0–3 rows of scales.

Orbital cirrus absent in some species, if present simple to palmate. Anterior nasal cirri simple to palmate, on posterior margin of a short tube.

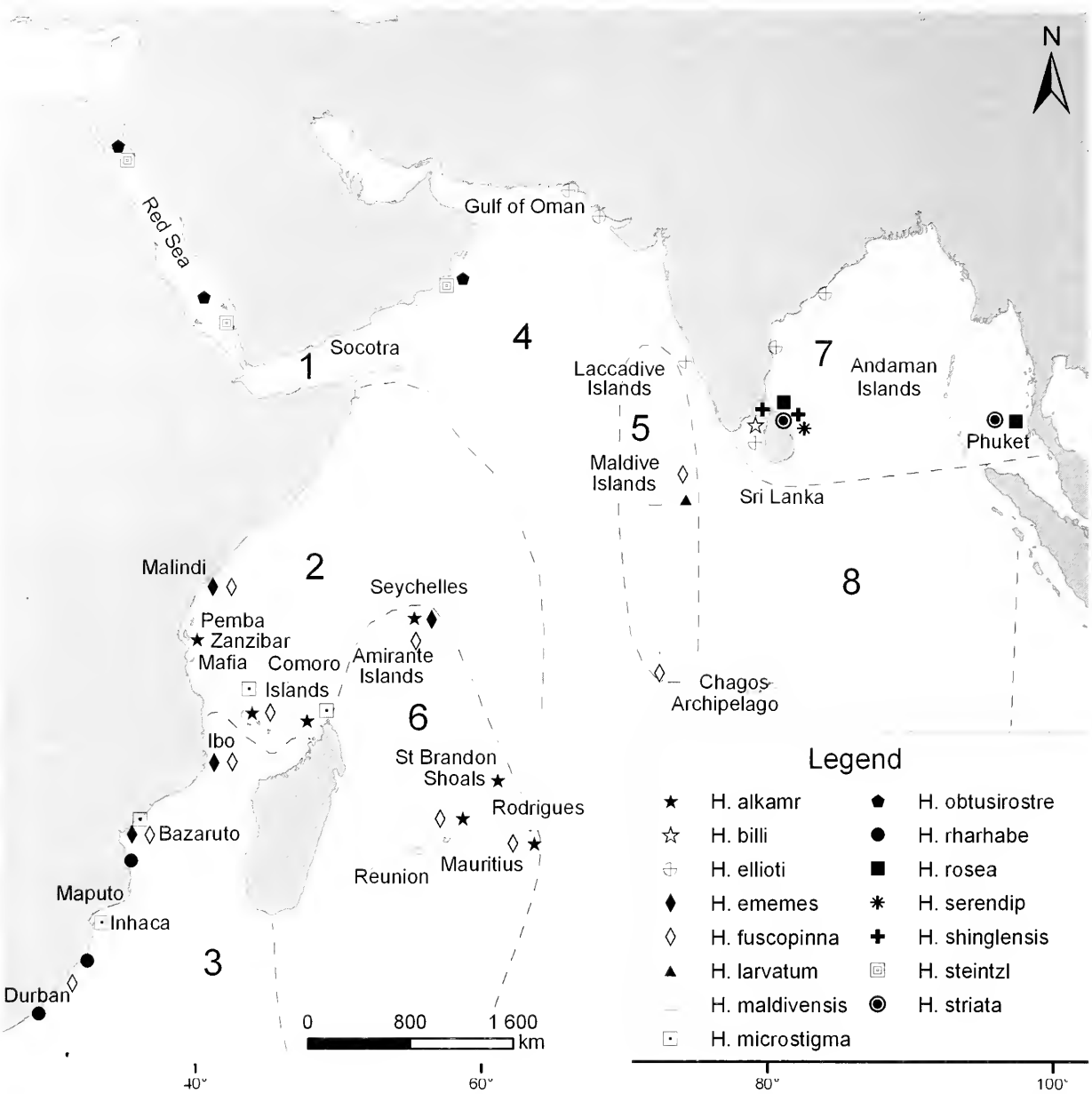


Fig. 1. Known distributions of Helcogramma species in the Indian Ocean. The biogeographic areas marked are demarcated as follows: 1 - Red Sea and Gulf of Aden, delimited by a line from eastern Yemen to Socotra to north-eastern Somalia; 2 - Somali Basin, bounded by Socotra in the north, the Comoro Islands and northwest Madagascar in the South, the Carlsburg Ridge in the northeast and the Mascarene Plateau in the southeast; 3 - Natal Basin - lying between Africa and Madagascar and bounded by the Comoro Islands in the north and the Madagascar Ridge in the southeast; 4 - Arabian Basin - bounded by the Socotra and the Carlsburg Ridge in the southwest and the eastern margin of the Arabian Basin (Laccadive Ridge); 5 - Chagos Plateau, including the Chagos Bank and the Chagos - Laccadive Ridge; 6 - Mascarene Plateau - bounded by Madagascar and the Farquhar Group in the west, the Saya de Malha Bank in the east and the Southwest Indian Ridge in the south; 7 - Andaman Basin - bounded by India and Sri Lanka in the west, by the Malay Peninsula in the east and the northern margin of the Ceylon Plain in the south; 8 - East Indian Basin - delimited by Sri Lanka to the northwest, Chagos-Laccadive Ridge in the west, the northern tip of Sumatra to the northeast and the Investigator Ridge to the east (after Santini & Winterbottom 2002).

Other sources:
The Times Atlas and Encyclopaedia of the Sea, ed. Alistair Cooper. 1983. Times Books, London.
The Times Atlas of the World. 1987. Times Books, London.

KEY TO THE WESTERN INDIAN OCEAN SPECIES OF *HELCOGRAMMA*

Where possible, characters have been selected from both males and females. Where this is not possible the colour characters used are those of mature males. The live colours of four of the fifteen species are unknown, and preserved colour patterns are used for those species.

1a Body with longitudinal lines or lines of dots and dashes 2
1b Body without lines or similar markings 3

2a Nape naked; pectoral-fin rays 15; body with 3 broken, pale, longitudinal stripes, one from top of head below second dorsal fin, one from posterior margin of eye to dorsal base of caudal fin, and one just below midline; both sexes reddish in life with white stripes and spots. .....*H. maldivensis* (Maldives)
2b Nape scaled; pectoral-fin rays 16; body with 3 longitudinal stripes, one from top of head to dorsal base of caudal fin, one from posterior margin of eye to mid-caudal-fin base, and one broad stripe below lateral line, with 6–7 spots between the lowermost two stripes. Both sexes reddish in life with bluish stripes and spots .....*H. striata* (Sri Lanka and eastwards)

3a Origin of first dorsal fin over posterior margin of preopercle, first two dorsal-fin spines closer together than half the distance between spines 2 and 3, fin triangular and same height or taller than second dorsal fin, membrane between first two dorsal-fin spines with many micro-melanophores, males in real life. 4
3b Origin of first dorsal fin behind posterior margin of preopercle; first dorsal fin not as above, usually lower than second, spines more evenly spaced 6

4a Anal fin with melanophores on entire fin; interorbital relatively broad, mean 15 in head length; pale saddles at end of second and third dorsal fins yellow or pink in life; LL usually with more than 25 tubed scales.....5
4b Anal fin with melanophores along margin only, interorbital relatively narrow, mean16.6 in head length; pale saddles at end of second and third dorsal fins white in life; LL usually with fewer than 25 tubed scales .....*H. steinitzi* (Red Sea and Oman)

5a Orbital cirrus pointed, about half pupil diameter; head profile relatively blunt, about 70°; pale (yellow in life) saddles without micromelanophores at ends of second and third dorsal fins .....*H. microstigma* (Comoro Islands, northern Madagascar, south to Bazaruto)
5b Orbital cirrus short, as wide as long, head profile relatively sharp, about 60°; pale (pink in life) saddles with micromelanophores at end of second and third dorsal fins .....*H. rosea* (Sri Lanka and Andaman Sea)

6a Pectoral-fin rays 15–16; anal fin rays <21; second dorsal fin spines usually <14, third dorsal fin rays usually <11 7
6b Pectoral rays 17; anal fin usually with 21 rays; dorsal fins usually III + XIV + 11;, large males with line of micro-melanophores from upper lip, below eye to opercle; in life males orange-pink with dark to black median fins, line below eye blue-white .....*H. fuscopinna* (WIO)

7a Symphyseal mandibular pores 3 or more 8
7b Symphyseal mandibular pores 1-2 10

8a Lateral-line scales <25, not to base of caudal fin 9
8b Lateral-line scales 33–37, running to caudal-fin base; mandibular pores 5–7 + 3-5 + 5–7; nape naked; in life males with red and blue-black head, dark blue ocellus on pectoral fin base and body reddish to orange, dorsal fins reddish, anal fin blue or dark .....*H. ellioti* (Sri Lanka, SW India)

9a Body of males with melanophores below lateral midline, with 2–3 broad bands above midline; peduncle entirely covered with melanophores, lower half of head black; in life top of head and nape to middle of second dorsal fin red, pelvic fins red .....*H. shinglensis* (Sri Lanka, SE India, Laccadives)
9b Body without dark pigment, only scattered melanophores; head below eye and bases of pectoral and pelvic fins with many melanophores; median fins without pigment except black spots on membrane between first two dorsal fin spines; in life brown with 3 narrow, white, slanted bands from dorsum to midline .....*H. ememes* sp. nov. (east coast of Africa, Seychelles)

10a Mandibular pores 2-3 + 1-2 + 2-3 11
10b Mandibular pores 4-6 + 1 + 4-6 12

11a Nape naked; lateral-line pored scales 21-22; second dorsal-fin spines 11-12 (usually 12); anal-fin rays 16-18 .....*H. larvata* (Maldives)
11b Nape scaled; lateral-line pored scales 28-33; second dorsal-fin spines 13; anal-fin spines 19-20 ....*H. billi* (Sri Lanka and eastwards)

12a Mandibular pores 4 + 1 + 4. 13
12b Mandibular pores 5-6 + 1 + 5-6 14

13a Body of mature males nearly all black with 2-3 pale narrow streaks from dorsum to lateral midline; median fins dark to black; in life bases first and second dorsal fins yellowish-green, eye red, snout green, anterior dorsum reddish; blue line from corner of mouth to posterior margin of pre-opercle .....*H. obtusirostre* (Red Sea, Oman)
13b Body of males pale with 7-8 clusters of melanophores along midline, head below eye black, colour stopping abruptly between isthmus and ventral fin base; fine cirri on frontal behind eyes .....*H. serendip* sp. nov. (Sri Lanka)

14a Body of males nearly black with 3-4 pale narrow streaks from dorsum to midline, dorsal fins with dark margins, anal fin densely covered with melanophores, upper lip dark in centre, with clear halfmoon-shaped patches either side; in life with 6-7 silvery white spots along mid-side, blue line from corner of mouth to posterior margin of opercle, with bright crimson on upper lip on either side .....*H. rharhabe* sp.nov. (east coast of Africa - East London, South Africa to Bazaruto, Mozambique)
14b Body of males pale with scattered melanophores and 7-8 clusters of melanophores along mid-side, head below eyes black, colour continuing onto pectoral and ventral fin bases .....*H. alkamr* sp. nov. (Comoro Islands, Seychelles, Mauritius)

SPECIES ACCOUNTS

Helcogramma alkamr sp. nov.

Figs. 1 & 2, Plate 1

Helcogramma chica non Rosenblatt in Schultz 1960: 294-297, fig. 114; Hansen 1986 (in part).

Holotype. ROM 73734; 27.5 mm SL male; Mayotte, French Territory Community, north coast of Isle Malandzamuzatsinsi (12° 40′ 19″ S, 44° 03′ 26″ E); intertidal - depth, 1m; coral rock and rubble with sand patches and algae; collected R. Winterbottom et al., 17 November 1988; field number RW 88-21.

Paratypes. **Mauritius**: AMS 42910-001 (5: 23.1-26.4 mm); SAIAB 70665 (23: 11.0-26.8 mm). **Comoro Islands**: BMNH 2004.1.6.11-15 (5: 19.9-25.7 mm); ROM 73735 (16: 15.6-26.5 mm) & ROM 73736 (23: 14.1-25.8 mm); USNM 375015 (5: 21.5-25.6 mm); USNM 228984 (7: 28.3-36.5 mm). **Seychelles**: SAIAB 70664 (26.0 & 29.7 mm); USNM 228973 (5: 24.6-28.6 mm), and USNM 261389 (38: 20.8-31.4 mm), Aldabra Atoll. **St Brandon Shoals**: SAIAB 1915 (5: 21.8-28.3 mm); USNM 222359 (6: 25.8-31.8 mm). **Tanzania**: USNM 222365 (20: 16.1-27.0 mm), Latham Island. **Madagascar**: USNM 382859 (3: 19.7-27.8 mm), Nosy Bé.

DIAGNOSIS. A medium-sized species of *Helcogramma*, less than 40 mm SL, with low first dorsal fin, naked nape, males brown in life with red-brown bars from dorsum to lateral midline, with small white spots along lateral midline, and usually 5 + 1 + 5 mandibular pores.

DESCRIPTION. Dorsal fins III + XIII-XIV + 10-11; anal fin I,19-20 (rarely 17 or 18, usually 19 rays - Table 2); pectoral fins 16: usually 1, 8, 7. Lateral line 19-25 (mode 21) pored scales, ending below the junction of the second and third dorsal fins; total lateral scales 36-39 (usually 37 or 38). Vertebrae 10 + 25-26 (rarely 24-1 of 15 counts); 0 (rarely 1) free pterygiophore between second and third dorsal fins. Mandibular pores 4-5 + 1 + 4-5 (usually 5 + 1 + 5; 6 + 1 + 6 for St Brandon Shoals specimens) (Fig. 2b). Head length 3.2-4.1 (3.7) in SL; eye 2.4-3.4 (2.9), maxilla 2.0-2.6 (2.3) in head length; snout short, profile blunt, 63-78° (71°).

Nape naked, but with patches of scales above first few lateral-line scales; 2-3 rows of scales on base of caudal fin; scales do not extend to bases of first and second dorsal or anal fins; no scales on underside of caudal peduncle. Posterior margin of eye with small spines on edge of frontal bones (Fig. 2c). First dorsal

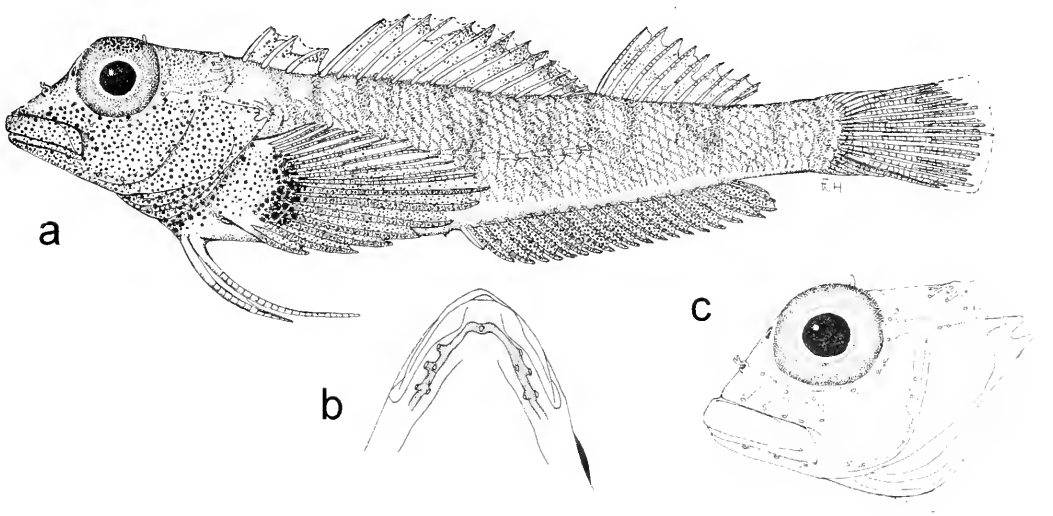


Fig. 2. *Helcogramma alkamr*. **a**, holotype, ROM 73734, male, 27.5 mm SL, Mayotte, Comore Islands; **b**, mandibular pores; **c**, head showing small spines on posterior margin of eye.

fin less than half height second dorsal fin. Pelvic fins united by membrane for length of shorter, half length of longer ray, longest ray reaching about half distance to vent. Labial folds moderate. Broad patch of teeth in front of both jaws, single row at sides, with row of enlarged teeth inside middle of upper jaw, both outside and inside middle of lower jaw. Maxilla reaches vertical through anterior of orbit; orbital cirrus small and pointed. Interorbital width a little less than pupil diameter.

Live colour. Males (from photograph of a male from the Comoros by R. Winterbottom) with pale brown body with pairs of reddish-brown short bars from dorsum to lateral mid-line, with many small white spots between. Along mid-line series of dark brown blotches with smaller bluish-white spots between. Body below midline pinkish. Dark brown band at base of caudal peduncle. Head spotted with red-brown and black, darker below lower margin of eye. Eye red and pale gold. Pale blue line from corner of mouth onto preopercle. Pectoral-fin base and base of lower fin rays darkly spotted with black, interspersed with pale blue and brown. Pelvic fins pink. First dorsal fin with pink and black spots; second with four narrow bands of pink and black spots; third similar but lighter. Caudal fin without colour; anal fin grey.

Females (from a photograph of a female from the Seychelles by Phil Heemstra) with creamish body with six pairs of semi-bars, those below first two dorsal fins tending to coalesce, darkest pair across peduncle, and those below end of second and third dorsal fins extending to anal-fin base. Head whitish with brown spots and orange blotches, darkest on top and on opercle; snout brown; orange and silver-white. First dorsal fin with orange on middle of membrane between first two spines and black spots on middle of other membranes; second dorsal fin with bands of orange and black spots similar to males; third dorsal fin pale orange bands. Anal fin with orange along margin with black on the membranes. Caudal fin with pinkish- orange marks in centre and along margin. Lower rays of pectoral fins pale orange distally and brown at base, membranes immaculate; pelvic fins white.

Colour in alcohol. Males: head with evenly-spaced melanophores and dark brown 'rosettes' from upper lip, below eye, onto pectoral-fin base throat and extending to base of pelvic-fin. Top of head, interorbital and snout with smaller melanophores. Some body scales with small melanophores on scale margins, pigmentation heaviest above midline, giving some suggestion of broad bands which may join on the midline to form V- or Y-shapes (as illustrated), but often only form a series of 8 clusters of spots along the side from beneath the pectoral fin onto the caudal peduncle, darkest anteriorly. Pectoral fin with dark to black half-moon or triangle, apex extending from base of rays one-quarter length of central rays; lower (undivided) rays with many, small melanophores on elements and membranes. First dorsal fin with scattered melanophores, darkest on margin; second dorsal fin with brown spots anteriorly and black spots posteriorly, fin darkest along the margin; third dorsal fin with scattered melanophores, forming 3 indistinct rows on some specimens. Anal fin evenly and densely spotted with melanophores, those on elements smaller and more dense than on membranes. Pelvic-fin rays distally with a line of small melanophores on outer edges of rays.

Females with 6 or 7 brown semi-bars on body above midline, 1 to 3 or 4 below second dorsal fin, 5 and 6 below third dorsal fin, 1 or 2 on caudal peduncle,

forming 8–10 brown blotches along midside. Top of head and interorbital with small melanophores, opercle and pectoral-fin base with scattered melanophores, small cluster of melanophores below eye and line of small spots from eye onto upper lip. First dorsal fin with small melanophores on membrane between first two spines; second dorsal fin with scattered spots; third dorsal and caudal fins immaculate. Anal fin with line of small melanophores on distal half of rays. Pectoral-fin rays brown at the base and with small melanophores on lower, undivided rays that suggest 2 or 3 broad bands.

DISTRIBUTION (Fig. 1). *Helcogramma alkamr* is currently known from the Comoro Islands, northern Madagascar, Zanzibar, Seychelles, St Brandon Shoals, Mauritius and Rodrigues.

ETYMOLOGY. 'al-Kamr' or al-Qumr is the original Arabic name for Madagascar (*Jazirat al-Qumr*), which became transferred to the Comoro Islands by the historian Ahmad Ibn Mājid in the 15th century. Today Comorians accept this is the origin of the name for their islands and from it the English name is derived. The specific epithet is used as a noun in apposition.

COMPARISONS. The blue line running from the corner of the mouth onto the preopercle suggests that *Helcogramma alkamr* is one of the *H. obtusirostre* species group. Further investigation is, however, required to confirm this.

In the Comoro Islands *H. alkamr* occurs sympatrically with *H. microstigma*, in the Seychelles with *H. ememes* and in both localities with *H. fuscopinna*. *H. alkamr* lacks the blue-white line under the eye characteristic of *H. fuscopinna*, and the tall first dorsal fin of *H. microstigma*, with micro-melanophores on the membrane between the first two spines. It can be distinguished from *H. ememes* by having 16 vs 15 pectoral-fin rays and a single symphyseal mandibular pore vs 3 in *H. ememes*.

REMARKS. Both males and females from the Comoro and Seychelles Islands are more heavily pigmented than specimens from Mauritius, which have only a few scattered spots on the body. The lower pectoral-fin rays of Comoro Islands males are less pigmented than in Mauritius males, while the caudal fin of Mauritius males often has a narrow black stripe at the base, absent in males from the Comoro Islands. The body bars of Comoro Islands females and the blotches along the body are much more distinct than in females from Mauritius. Furthermore, specimens from the Comoro Islands predominantly have 25 caudal vertebrae, while those from Mauritius have 26 (Table 2).

These differences may be the result of local environmental differences: the specimens from the Comoro Islands were collected in turbid water, one collection in less than 3m in depth and another in 0–20m depth, amongst coral rock and rubble with some sand, while those from Mauritius were collected in clear water, 3–5m in depth, in a high energy tidal environment amongst large boulders and coral heads.

Table 2. Counts for *H. alkamr* sp. nov. from different localities.

	D2 spines			D3 rays		Anal-fin rays				*Caudal vert.					Lateral line scales						
	12	13	14	10	11	17	18	19	20	24	25	26	27	28	19	20	21	22	23	24	25
Latham Is. Tanzania n=21		9	12	15	6			21			1	17	2		1	2	10	3			
Comoro Islands n=29		12	17	20	9	1	3	22	3		1	19	5			8	15	4	1		
Nosy Be, Madagascar n=5			5	1	4		1	2	2						1		1		1		1
Seychelles n= 45		17	28	27	18		3	39	2		2	15	1		1	2	17	13	7	3	
Mauritius n=25	1	3	17	3	18			10	10			6	18	1		4	7	5			
St Brandon Shoals n=12		7	5	1	11			6	6				7				4	6	2		

* Counts of 25 (26 for Mauritius) caudal vertebrae usually the result of 2 fused vertebrae

Helcogramma billi Hansen
Figs. 1 & 3

Helcogramma billi Hansen 1986: 329, fig. 10 (Sri Lanka).

DIAGNOSIS (Partially from Hansen 1986). Dorsal fins III + XIII–XIV + 9–11 (usually III + XIII + 10–11); anal fin I,17–20 (usually 19–20 rays); pectoral fins 16: 2, 7, 7. Lateral line 27–33 (usually 30) tubed scales ending below middle of third dorsal fin; total lateral scales 38–39. Vertebrae 10 + 25–26; 1 free pterygiophore between second and third dorsal fins. Mandibular pores 2–3 + 1 + 2–3 (Fig. 2b) Head length 3.4 in SL; eye 2.8, maxilla 2.2 in head length.

Nape scaled; no scales on base of caudal fin; scales do not extend to base of anal fin anteriorly. Pelvic fins united by membrane for 2/3 length of shorter ray, longest ray reaching vent. First dorsal fin half height of second, higher than second in males from the Comoro Islands (see REMARKS below). Maxilla reaches vertical through middle of pupil; orbital cirrus a small, rounded flap.

Live colour. Not known.

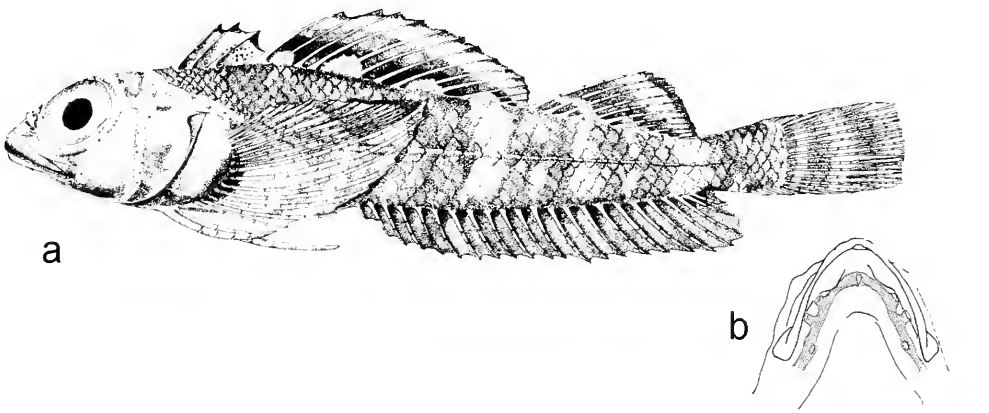


Fig. 3. *Helcogramma billi*. **a**, paratype, USNM 222368, male, 31.0 mm SL, Trincomalee, Sri Lanka (from Hansen 1986); **b**, mandibular pores.

Colour in alcohol. Body of males with 5 darkish 'H'-shaped bars which form a series of darker spots along midline. Occiput, head below eyes to pelvic- and pectoral-fin bases evenly covered with small melanophores. First dorsal fin membrane between first and second spines dark; second dorsal fin with thin black margin, a clear stripe beneath, and irregular black marking along middle (Hansen, 1986: 329: to form "4 distinct clear areas basally on fin elements 2, 5, 9 and 11."); third dorsal fin irregularly banded; anal-fin membranes dark, uniformly spotted with black. Pectoral fins with dark brown half moon at base of middle rays and with 3 broad, chevron-shaped, brownish bands, first in middle of fin, last at tips of rays, second between them; pelvic-fin rays dark; caudal fin with 2-3 dark vertical bands.

Females and juveniles less heavily pigmented and with little or no pigment on head below eyes.

Distribution (Fig. 1). *Helcogramma billi* is currently known only from Sri Lanka, although the species may be more widespread. It was not recorded from the Maldives by Fricke & Randall (1992), but may be found in the Andaman Islands, an area whose shore fishes are not well known.

Comparisons. There are six Western Indian Ocean species of *Helcogramma* with a scaled nape: *H. billi, H. maldivensis, H. rosea, H. striatum, H. steinitzi* and *H. microstigma*. ***H. billi*** can easily be distinguished from *H. maldivensis* and *H. striatum* as these two species are very distinctly striped, while *H. steinitzi* has fewer lateral-line scales (21-27, mean 25 vs 27-33, mean 30 for *H. billi*) and *H. steinitzi* does not occur sympatrically with *H. billi*. However, *H. billi* and *H. rosea* do occur sympatrically, but can be separated on mandibular pore counts and colour pattern-see under *H. microstigma*.

Material examined. **Sri Lanka**: SAIAB 30432 (21.0 & 22.3 mm) and SAIAB 30433 (3: 25.2-27.3 mm).

Helcogramma ellioti (Herre)

Figs. 1 & 4. Plate 1

Helcogramma ellioti (Herre 1944: 49) (Madras Coast, India); Lal Mohan 1968: 124; Shamsul Hoda 1983: 41, fig. 1; Hansen 1986: 335 (in part: India and Sri Lanka). *Helcogramma indicus* Talwar & Sen 1971: 249, fig. 1 (Cape Comorin, South India).

Diagnosis (Partially from Hansen, 1986). Dorsal fins III + XIII + 9-10; anal fin I, 18-20 (usually 18 rays); pectoral fins 16: 1, 8, 7. Lateral line 33-37 pored scales ending close to or at the base of the caudal fin; total lateral scales 36-38 (usually 38). Vertebrae 10 + 24-25; 1 free pterygiophore between second and third dorsal fins. Mandibular pores 5-7 + 3-5 + 5-7 (Figs. 4c & d). Head length 3.3-3.7 (3.5) in SL; eye 2.6-3.0 (2.8) in head length; maxilla 2.2-2.4 (2.3) in head length.

Nape and belly naked, scales do not extend to base of anal fin; 1 row of scales on base of caudal fin. Pelvic-fin rays united by membrane for half length of shorter ray, longest ray reaching about 3/4 distance to vent. First dorsal fin of males same height as second, about height of second in females. Mouth reaches vertical through middle of pupil; orbital cirrus flat and palmate.

Live colour (from colour photograph by J.E. Randall). Body of males grey-brown with three pale saddle-like areas, first below middle and second below end of second dorsal fin, third below end of third dorsal fin; belly pink; top of head dark brownish, becoming red at level of eye, a bright white area on the "shoulder" above the pectoral-fin base. Head below level of eye, black and blue, colour not extending to pelvic-fin base; branchiostegal membranes blue and black; narrow, blue line from hind end of maxilla onto preopercle; eye, snout, interorbital and area behind eye deep red. First dorsal fin pale yellow with red spots on membrane behind third spine; second dorsal fin mostly translucent with pale blue basally; third dorsal

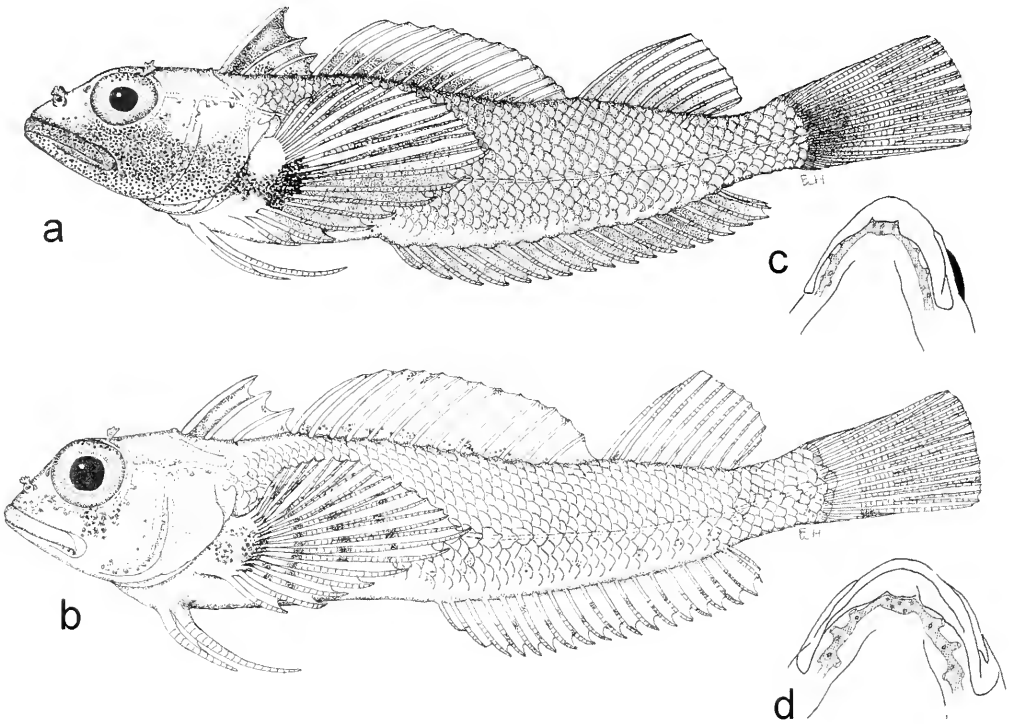


Fig. 4. *Helcogramma ellioti*. **a**, SAIAB 30431, male, 29.3 mm SL, Hikkaduwa, Sri Lanka; **b**, female, 28.0 mm SL; **c & d**, mandibular pores.

fin mostly pale blue with white distally on anterior rays. Anal fin pale blue-grey. Pectoral fins with deep blue ocellus surrounded by black at base of middle rays, with crimson above and below and blue and black on base of fin, rays with irregular darker and paler bars. Pelvic-fin base and rays crimson; caudal fin pale blue-grey.

Females with whitish body with brown marks forming oblique semi-bars and blotches from dorsum to below lateral midline. Head below eye white with brown and red spots, above darker with brown blotches and a brown line from corner of eye onto upper lip; eye pale gold. First dorsal fin pale anteriorly brown, posteriorly translucent; second and third dorsal translucent with pale gold and white marks. Anal fin white with narrow brown marks on rays forming oblique bars. Upper, divided rays of pectoral fins banded light brown and pale gold, lower, undivided rays gold with dark brown marks on rays. Pelvic fins white; caudal fin translucent with white at base of rays and bright white line at margins of hypural plates.

Colour in alcohol. Body of males, except belly, with even scatter of melanophores. Lower portion of head from upper lip, below eye and onto opercle and branchiostegal membranes dark grey to black; isthmus and pelvic-fin base immaculate. Top of head with fine spots; snout immaculate; oval, unpigmented area behind eye which extends onto the upper portion of opercle. Pectoral-fin base with dark triangular mark, apex posterior, with a circular, black spot at base of middle rays. Fin clear above and below spot, below which the rays are dusky and above which they are spotted with small melanophores. First dorsal-fin membrane between spines 1 and 2 dusky; second dorsal fin with basal dark band and thin, dark band along margin; third dorsal fin with dusky basal band; anal fin dusky; diffuse dark area at base of caudal fin.

Females with diffuse dark bars on body; top of head, cheeks, snout and opercles with scattered melanophores, area below eye, including maxilla, immaculate; first dorsal-fin membrane between first two spines dusky; second dorsal fin with faint basal and marginal bands; third dorsal, anal and pectoral fins banded, colour on elements only; caudal fin with narrow, clear band basally and dusky area postero-dorsally, colour only on rays.

DISTRIBUTION (Fig. 1). The species has been recorded from either side of the Indus Delta in tide pools on the Karachi and Gujerat coasts, from Kerala, Sri Lanka and the east and northeast coasts of India.

COMPARISONS. *Helcogramma ellioti* occurs sympatrically with *H. billi* , *H. rosea*, *H. serendip* and *H. shinglensis*. Like *H. billi*, *H. ellioti* has a long lateral line that extends onto the caudal peduncle, but has a naked nape, scaled in *H. billi*. *H. ellioti* and *H. shinglensis* have similar live colours, with an ocellus on the pectoral-fin base and red above the eyes and blue-black below (in

males). *H. shinglensis* has fewer tubed lateral-line scales-21-24, vs 34-35 for *H. ellioti* and a lower first dorsal fin. *H. ellioti* is quite different in colour to *H. rosea* and lacks the micro-melanophores on first dorsal fin of *H. rosea*. *H. ellioti* can be distinguished from *H.serendip* by its long tubed lateral line-33-37 scales vs 20-22 for *H. serendip*.

Remarks. In her revision of the genus Hansen (1986: 336) states that *H. ellioti* has a mandibular pore pattern of 3 + 1 + 3, which is surely in error. The holotype (SU 38840) has a pore pattern of 6 + 4 + 6, and a paratype (SU 38841) of 6 + 4 + 7 (Catania, pers. comm.) However, the pore pattern of one or more as yet undescribed species (previously misidentified as *H. ellioti*) from the Western Pacific Ocean has a pore pattern of 3-4 + 1 + 3-4. As Hansen considered the Western Pacific specimens to be *H. ellioti*, and this would explain her incorrect description.

H. ellioti, together with *H. obtusirostre* and *H. rharhabe* (and possibly *H. alkamr*) belong to a complex, which includes several species in the Western Pacific Ocean and one in the South Atlantic. These species share at least one putative synapomorphy-a blue line that runs from the lower lip, through the corner of the mouth to the hind margin of the preopercle in mature males.

The above three species can be separated from each other on the basis of colour (*H. rharhabe* has a crimson patch on the upper lip, absent in the other two species), and by mandibular pore patterns (*H. ellioti* has 3-5 symphyseal mandibular pores vs 1 only for the other two species).

Material examined. **Sri Lanka**: SAIAB 30434 (31.6 mm); SAIAB 30431 (3: 28.0-31.0 mm); USNM 276540 (26.8 & 27.1 mm),

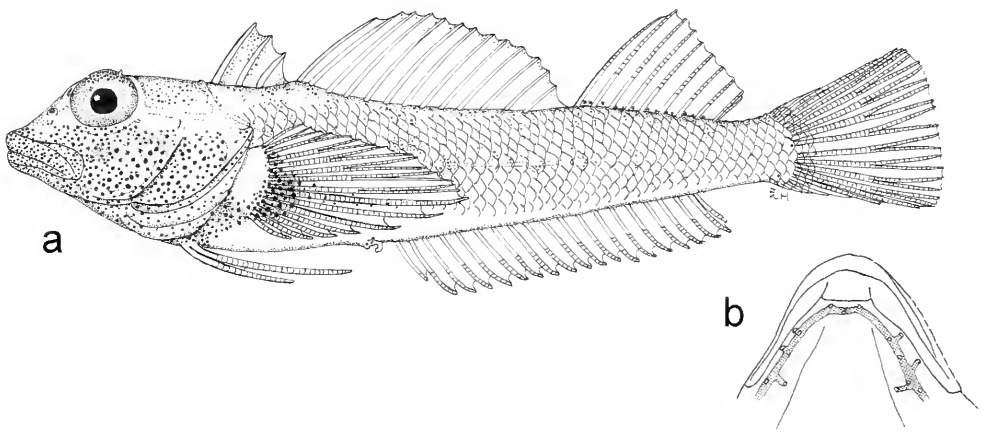


Fig. 5. *Helcogramma ememes*. **a**, holotype, SAIAB 70605, male, 28.9 mm SL, Ibo Island, Mozambique; **b**, mandibular pores.

***Helcogramma ememes* sp. nov.**
Figs. 1 & 5, Plate 1

Holotype. SAIAB 70605, 28.9 mm SL male, Ibo Island, Mozambique (12°24′ S, 40°34′ E); collected by J. L. B. Smith, August, 1951.

Paratypes. **Mozambique**: BMNH 2004.1.6.7-8 (26.8 & 29.2 mm), Ibo Island; ROM 73756 (28.8 & 30.2 mm), SAIAB 70739 (39.1 mm) and SAIAB 7449 (14: 22.1-29.1 mm), Bazaruto Island; SAIAB 30398 (23.8 mm), Baixo Pinda; SAIAB 30401 (14: 17.1-33.1 mm) and USNM 375016 (4: 25.3-27.0 mm), Ibo Island; SAIAB 4274 (29.5 mm), Porto Amelia. **Seychelles**: ROM 73757 (4: 22.9-27.4 mm), SAIAB 30417 (19: 17.9-24.1 mm), AMS 42920-001 (3: 19.3-21.3 mm) and BMNH 2004.1.6.9-10 (24.0 & 29.1 mm), all from Mahé; BPBM 39290 (20.2 & 20.8 mm), Aride; SAIAB 30406 (4: 24.5-26.2 mm), La Digue; SAIAB 54500 (23.4 & 26.6 mm), Isle Cousine. **Kenya**: SAIAB 30407 (26.5 & 26.8 mm) and SAIAB 30409 (4: 21.6-24.1 mm), Malindi.

Diagnosis. A medium to large species of *Helcogramma* with three symphyseal mandibular pores, low first dorsal fin and lateral line that ends anterior to or below junction of second and third dorsal fins. Males brown in life with three narrow white saddle marks on body and with lower half of head black.

Description. Dorsal fins III + XIII-XIV + 10-11 (2 of 78 with XII D2 spines and 5 of 72 with 9 rays), usually III + XIII + 10; anal fin I,18-20 (4 of 78 with 20 rays), usually 19 rays; pectoral-fin rays usually 15: 1, 7, 7 for east coast of Africa, 1, 8, 6 or 2, 7, 6 for Seychelles. Tubed lateral-line 19-23, mode 21; total lateral scales 36-38, transverse scales 9/7. Vertebrae 10 + 24-27 (usually 25; 1 with 24 and 1 with 26 of 8 counts);1 free pterygiophore between second and third dorsal fins.

Table 3. Counts for *H. ememes* sp. nov. from different localities.

Locality	D2 spines			D3 rays			Anal fin rays			Lateral line scales					Pectoral-fin rays			**Caudal vertebrae					Free pter.	
	12	13	14	9	10	11	18	19	20	19	20	21	22	23	1,7,7	1,8,6	2,7,6	n	24	25	26	27	0	1
Seychelles n=28*		23	5	2	25		13	12	2	2	8	8	4	3	1	13	9	12	1	2	9		4	8
Malindi n=13	1	8	1		5	2		4	1		1	2	2		8			6		1	4	1		
Ibo Island n=14		14		1	12	1	3	11		1	2	3	3		9	1		7			6	1		7
Porto Amelia n=1		1			1			1							1			1				1	1	
Baixo Pinda n=1		1			1			1							1			1			1			1
Bazaruto n=16	1	14	1	1	15		2	14		3		6	2	2	13	1		1			1			1

* One aberrant specimen with 8 D3 rays and 17 anal-fin rays
** count of 24 result of 3 fused vertebrae
† Most common arrangement; a few specimens have 2,6,6 2,6,7 1,8,7 or 1,7,8 rays.
pter. = pterygiophore

Table 4. Morphometric data for *H. ememes* sp. nov. from different localities.

Locality	SL/Head length			Head length/eye diameter			Head length/maxilla length		
	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
Seychelles n=28	3.6-4.2	3.9	0.17	2.3-3.4	3.0	0.25	2.3-3.3	2.5	0.27
Malindi n=11	3.3-3.9	3.6	0.16	2.6-3.0	2.9	0.16	2.3-2.6	2.4	0.10
Ibo Island, Porto Amelia, Baixo Pinda n=16	3.4-4.0	3.6	0.15	2.7-3.1	3.0	0.13	2.2-2.6	2.3	0.11
Bazaruto n=16	3.4-3.8	3.5	0.09	2.6-3.3	2.9	0.17	2.2-2.5	2.4	0.08

Mandibular pores 4–7 + 3 + 4–7 (rarely 7 pores; Fig. 5b). Head length 3.6–4.2 (3.9), Seychelles, or 3.3–4.0 (3.6), east coast of Africa; eye 2.3–3.4 (3.0) in head length; maxilla 2.2–3.3 (2.4) in head length (see Table 3).

Nape naked; body scales do not extend to base of second dorsal or anal fins; ventral surface of caudal peduncle with thin scales. Two scale rows at base of caudal fin. First dorsal fin low, about half height of second. Pelvic-fin rays united by membrane for half length of shorter ray, longest ray reaching vent in males, about 20% shorter in females. Maxilla reaches vertical through anterior of pupil. Orbital cirrus small and pointed, often with micro-melanophores.

Live colour (based on a colour slide by J. E. Randall of a male and female from the Seychelles). Head of males below eyes with densely packed melanophores, which extend to posterior margin of opercle and to base of pelvic fins; above reddish with scattered melanophores. Eye orange-red, lower lip with some white. Body mid-brown with three narrow, white and pink saddles, extending to midline, the first below middle of second dorsal fin, second below end of second dorsal fin and third below end of third dorsal fin. Below midline a series of six or more rounded, white blotches of varying size, interspersed by diffuse darker brown areas with melanophores; belly white. First dorsal fin transparent, with some brown on spines and a white mark on membrane between first two spines; second and third dorsal fins transparent with brown and white marks on spines. Caudal fin largely translucent, cream at base with three red-brown marks, one dorsally, one centrally and one ventrally. Anal-fin membranes translucent, rays pink with fine melanophores. Pectoral-fin bases with a yellow blotch centrally, with white marks above and black and blue pigments below; proximal portion of central rays with an oval of dense melanophores, rays pink above and with red spots below the black, distal portion of fin transparent. Pelvic fins pink.

Females with dull, olive-green body with brown and white marks dorsally and a series of six or more rounded, white blotches of varying size below midline, interspersed with brown blotches. Head below level of eye white with brown marks, above darker olive green with brown marks, eye yellowish. All fins transparent with white marks, but pectoral fin bases and proximal portion of rays with brown and white marks.

Colour in alcohol. Males retain the melanophores on the lower portion of the head and to bases of pelvic and lower part of pectoral fins. Top of head with small melanophores. Small melanophores on body suggest bands and form loose clusters along midline. Some specimens have a small saddle of melanophores at posterior end of third dorsal fin. Pectoral fins with a black 'D'-shaped cluster of melanophores proximally. First dorsal fin with brown spots on membrane between first two spines.

Females with scattered clusters of brown spots on body, mostly along anterior lateral midside. Top of head , below eye and opercle with small brown spots; line of brown to black spots from each eye onto upper lip. First dorsal fin with a few black or brown spots on membrane between first two spines, spines with black spots; second, third and caudal fins with thin brown or black line along each element; caudal fin with thin brown band at base and brown or black lines along rays; pectoral fin with four irregular brownish bands, pigment on rays only.

Etymology. The name is taken from the initials of Margaret Mary Smith, often called MMS. When I was a graduate student in the mid-1970s Margaret brought me into the J. L. B. Smith Institute, of which she was then Director, for two years on "soft money". Thus started my interest in fishes and fish taxonomy. I learned only recently that she in fact paid me out of her own pocket. In gratitude I am pleased to be able to name one of "my" little fishes in her memory and for her generosity. Many of the specimens of this species were collected by Margaret and J. L. B. Smith in the 1960s. The specific name is used as a noun in apposition.

Distribution (Fig. 1). The species has been recorded from the Seychelles and various localities along the east coast of Africa between Malindi, Kenya (3°14'S) and Bazaruto, Mozambique (21°38'S).

Comparisons. *Helcogramma ememes* occurs sympatrically with *H. alkamr* and *H. fuscopinna* in the Seychelles and on the east coast of Africa its range overlaps that of *H. rharhabe* at Bazaruto. *H. ememes* can be distinguished from *H. alkamr* by its symphyseal pores, 3 vs 1 in the other two species (see REMARKS below also). It can be distinguished from *H. fuscopinna* by the absence of the blue-white line below the eye of males and large females of that species.

The fin element, scale and pore counts of *H. ememes* are identical to those of *H. shinglensis*, which is known only from Sri Lanka and SE India, but the latter species lacks scales on the ventral surface of the peduncle and males have a completely different colour pattern-see under *H. shinglensis*.

Remarks. There are what may be significant differences between the specimens from the Seychelles and the east coast of Africa: those from the Seychelles have a smaller head than the specimens from the coast - mean 3.9 in SL vs 3.6 in SL and have a different pectoral-fin configuration (Table 3). While both have 15 rays, those from the Seychelles generally have the lowermost 6 rays undivided, whereas those from the coast have the lowermost 7 undivided. From the tripterygiid material I have examined over the years, this character is fairly consistent for a species. However, in all other characters examined, specimens from the two areas appear to be the same and, until live colour for east African material is available, they are considered as one and the same species.

H. alkamr and *H. ememes* males are very similar in colour and may be sibling species. They differ in that *H. ememes* lacks the blue line below the eye of *H. alkamr*; and *H. ememes* has 3 distinct white and pink saddle marks whereas *H. alkamr* has only lighter areas with white spots between short, brown bars. They also differ in mandibular pore pattern and in pectoral-fin ray counts: 16 for *H. alkamr* and 15 for *H. ememes*.

Helcogramma fuscopinna Holleman

Figs. 1 & 6; Plate 1

Helcogramma fuscopinna Holleman 1982: 115, fig. 4 (in part KwaZulu-Natal, South Africa); Hansen 1986: 337 (in part); Williams & McCormick 1990: 1020; Williams & Howe 2003:163.

Diagnosis (from Holleman 1982 and Williams & McCormick 1990). Dorsal fins III + XIII-XV + 10-12 (usually XIV+11); anal fin I, 19-21 (usually 21 rays); pectoral fins 17: usually 1, 9, 7. Lateral line 22-30 tubed scales ending below the anterior half of the third dorsal fin; total lateral scales 38-40 (usually 39-40)-see Table 5 for geographic variation. Vertebrae 10 + 27 (rarely 26 or 28); 1 free pterygiophore between second and third dorsal fins. Mandibular pores 5-8 + 1-2 + 5-8 (Fig. 6b). Head length 3.1-3.7 (3.4) in SL; eye 2.6-3.4 (2.9) in head length; maxilla 2.0-2.4 (2.1) in head length.

Nape naked, scales do not extend to bases of first two dorsal and anal fins; single row of scales on base of caudal fin. Pelvic fin rays united by membrane for half length of shorter ray, longest ray nearly reaching vent. First dorsal fin of males about 4/5 height of second, slightly shorter in females. Mouth reaches vertical through middle of pupil; orbital cirrus simple.

Live colour. Males with orange-pink body, scales with row of small melanophores along posterior margin; small, dusky rosettes scattered over body, generally more densely below midline. Darkly pigmented specimens (mature males) with 5 or 6 grey-white blotches stippled with small melanophores above and below midline, which may produce faint, vertical banding or narrow, dusky triangular marks, apex up, along the ventral half of body. Head with broad, black band stretching from mouth, below eye, onto opercle and pectoral-fin base; throat without colour but with densely spaced melanophores extending to belly, along anal fin and to base of caudal peduncle; distinct blue-white line with very fine stipples from upper lip, running below eye onto opercle. First dorsal fin darkly speckled to nearly black; second dorsal dark to black, often with darker margin, third dorsal with dark to black; anal fin uniformly dark to black; pelvic fins finely stippled, darker basally; ventral rays of pectoral

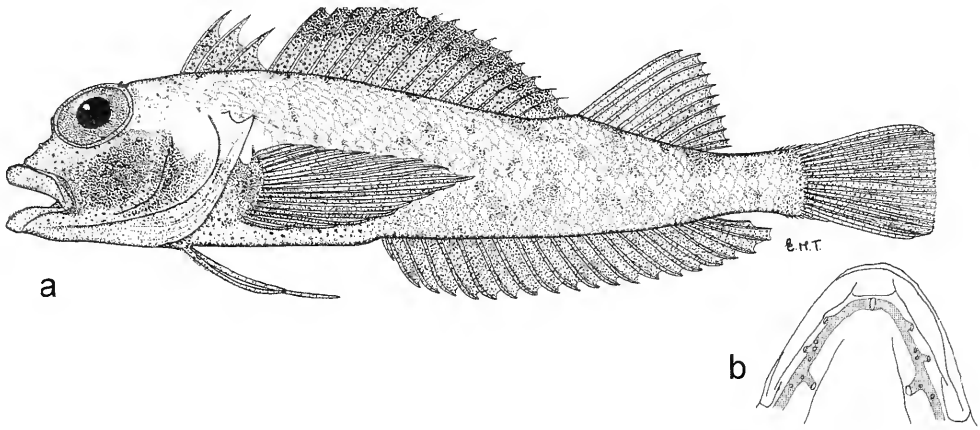


Fig. 6. *Helcogramma fuscopinna*. **a**, holotype, SAIAB 954, male, 37.6 mm SL, Sodwana Bay, South Africa; **b**, mandibular pores.

fins dark; caudal fin with uneven dark markings, mostly on membranes.

Females and immature specimens range from pale pinkish-orange with few melanophores to paler versions of large males, but without the heavy black on lower half of face. Large females also with blue-white line with micro-melanophores below eye.

Colour in alcohol. All colour is lost in preservative except the melanophores, the patterning on the body, the dark fins and line of fine stipples below the eye of males remaining distinctive. Females have no markings except for a few scattered brown spots and two small clusters just below the last elements of the second and third dorsal fins, and a line of micro-melanophores below the eye in large females.

DISTRIBUTION (Fig. 1). *H. fuscopinna* is known from the east coast of Africa from central KwaZulu-Natal to Kenya, Comoro Islands, Seychelles, Maldives, Chagos Archipelago, Mauritius and Rodrigues. It has not been recorded from Oman, Sri Lanka or India.

COMPARISONS. *Helcogramma fuscopinna* is the only member of the *H. fuscopinna* complex that occurs in the Western Indian Ocean. Mature males and large females can easily be distinguished from all other species by the blue-white line extending from the middle of the upper lip, below the eye and onto the opercle, which, in preservative, shows as a band of micro-melanophores. Individuals of all sizes also have generally uniform dark to black median fins not found in any other species.

REMARKS. *Helcogramma fuscopinna* is one of a complex of 11 species described by Williams & McCormick (1990) and Williams & Howe (2003) which occurs throughout the Indo-Western Pacific Ocean.

New material examined. **Mauritius**: SAIAB 70669 (44: 21.2–35.2 mm) and SAIAB 70672 (35: 15.8–37.3 mm). **Rodrigues**: SAIAB 70047 (18: 14.3–34.7 mm) and SAIAB 70245 (6: 27.9–33.9 mm). **Mozambique**: SAIAB 50596 (34: 23.4–35.6 mm), Malongane.

Table 5. Counts for *H. fuscopinna* from different localities.

Locality		D2 spines			D3 rays			Anal-fin rays				Lateral line scales										
		13	14	15	10	11	12	19	20	21	22	22	23	24	25	26	27	28	29	30	Mean	Mode
St Brandon Shoals	n=12		11	1	1	11			4	7			1	2	5	2	1				25	25
Mauritius	n=25	1	24		1	21	2		6	19			3	5	5	8	1		1		25	26
KwaZulu-Natal	n=51	2	47	2	10	41		1	11	36		3	6	12	9	3	1	1			24	24
Southern Mozambique	n=18	5	13		2	16			3	14	1		4	4	3	3	2	1		1	25	–
Bazaruto	n=6		6		3	3			1	5					2	1					25	25
Pinda	n=1	1				1				1					1						25	25
Mafia	n=12		12			1	11		2	10			1	4	3	2					25	24
Shimoni	n=5		4	1		5			1	4		1			2	1	1				25	25

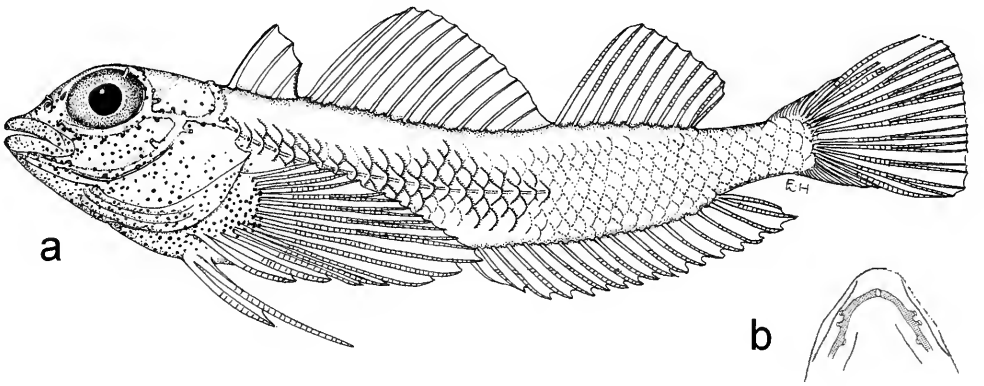


Fig. 7. *Helcogramma larvata*. **a**, paratype, BPBM 34519, 19.1 mm SL, North Male atoll, Maldive Islands; **b**, mandibular pores.

Helcogramma larvata Fricke & Randall
Figs. 1 & 7

Helcogramma larvata Fricke & Randall 1992: 6, figs. 5 & 6 (North Male Atoll, Maldives)

Diagnosis (from Fricke & Randall 1992). Dorsal fins III + XI–XII + 8–9; anal fin I,16–18; pectoral fins 15: 1, 7, 7. Lateral line 20–22 pored scales, ending below the first two rays of the third dorsal fin ; total lateral scales 32–35. Vertebrae 10 + 24–25. Mandibular pores 2–3 + 1 + 2–3 (Fig. 7b). Head length 3.5 in SL; eye 2.7, maxilla 2.1 in head length (derived from Fricke's measurements).

Nape and belly naked, scales do not extend to bases of first two dorsal and anterior of anal fins. Pelvic fin rays united by membrane for half the length of the shorter ray, longest ray reaching second to last ray of second dorsal fin. First dorsal fin half height of second. Maxilla reaches vertical through anterior margin of pupil; orbital cirrus small.

Live colour. Not known.

Colour in alcohol. "Head and body pale, lower sides of head in male dark, with light blotch below eye and two light blotches on pectoral-fin base; female with a few dark spots on side of head. Fins pale, except distal margin of the third D1 membrane in the male dusky." (Fricke & Randall 1992: 8).

Distribution (Fig. 1). Known from only four specimens from North Male Atoll, Maldives.

Comparisons. The species occurs sympatrically with *H. maldivensis*, from which it can readily be distinguished by colour, the latter species being striped, and with *H. fuscopinna*, which has dark fins and a blue-white line below the eye.

Material examined. BPBM 34510 (19.1 mm), Paratype, North Male Atoll, Maldives.

Helcogramma maldivensis Fricke & Randall
Figs. 1 & 8, Plate 1

Helcogramma maldivensis Fricke & Randall 1992: 9, figs. 7 & 8, plate 1 (Maldives).
Helcogramma striata Hansen 1986 (in part: Maldives)

Diagnosis (from Fricke & Randall 1992). Dorsal fins III + XII–XIV + 9–11 (usually III + XIII + 10); anal fin I,17–21; pectoral fins 15: usually 3, 6, 6 (SAIAB paratype 2, 6, 7). Lateral line 13–21 (usually 16–17) tubed scales, ending below first two rays of third dorsal fin ; total lateral scales 36–38 (usually 38). Vertebrae 10 + 25–26; 1 free pterygiophore between second and third dorsal fins. Mandibular pores 3 + 1–2 + 3 (Fig. 8b - Fricke & Randall record 3 + 2 + 3). Head length 3.4 in SL; eye 2.4, maxilla 2.3 in head length.

Nape scaled, belly naked, scales do not extend to bases of first dorsal and anterior of anal fins; 2 rows of scales on base of caudal fin. Pelvic-fin rays united by membrane for half length of shorter ray, longest ray reaching 5th from last ray of second dorsal fin. First dorsal fin half height of second. Maxilla reaches vertical through anterior margin of pupil; no labial flaps. Orbital cirrus absent.

Live colour. (From colour photograph by J. E. Randall.) Males with reddish-pink body, lower third light gray; sides with 3 lines of bluish-white dots or streaks which anteriorly form stripes, first running from first dorsal-fin spine to below centre of third dorsal fin, second from posterior margin of eye to upper base of caudal fin, third from top of pectoral-fin base to ventral side of caudal peduncle, dividing red upper part of body from grey lower part. Head reddish with small blue-white spots on snout and cheeks, lips orange-red, throat and isthmus white. Dorsal, anal and caudal fins carmine, colour on elements only, except for first dorsal fin which has white on the membrane between first two spines; pelvic and pectoral fins white.

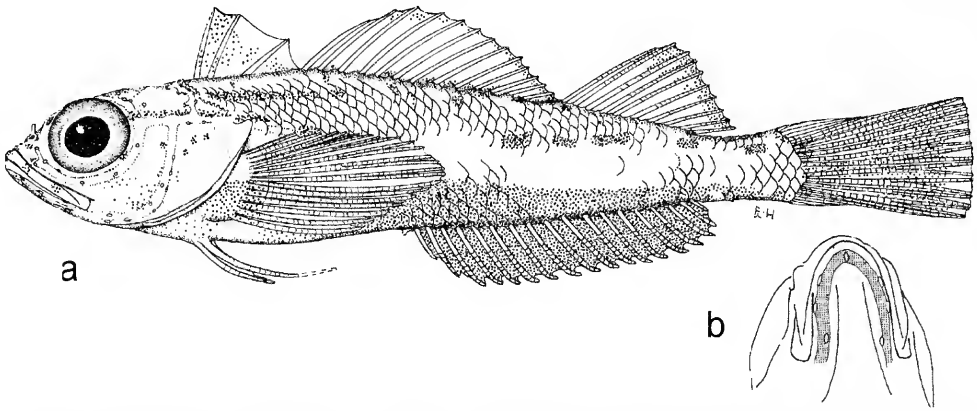


Fig. 8. *Helcogramma maldivensis*. **a**, paratype, SAIAB 36705, male, 20.3 mm SL, North Male atoll, Maldive Islands; **b**, mandibular pores.

Females lighter in colour than males, white ventrally, and lack the spots and stripes. Fins translucent.

Colour in alcohol. The colour fades to a pale straw, except for spots and stripes of males which become dark grey and are composed of micro-melanophores.

DISTRIBUTION (Fig. 1). *Helcogramma maldivensis* is currently known only from the Maldive Islands.

COMPARISONS. See under *H. larvata* above.

REMARKS. *Helcogramma maldivensis* is very similar to, and probably most closely related to *H. striata*, from which it differs in colour pattern (*H. striata* has three longitudinal bluish-white lines extending from base of caudal fin onto the head and is blue-green ventrally) and fewer pectoral-fin rays (15 for *H. maldivensis* vs. 16 for *H. striata*), and total lateral scales (36–37 for *H. maldivensis* vs. 38–39 for *H. striata*).

Material examined: SAIAB 36705 (20.6 mm), Paratype, North Male, Maldives.

Helcogramma microstigma Holleman
Figs. 1 & 9, Plate 1

Helcogramma microstigma Holleman 2006: 92, figs. 1, 2 & 5 (Bazaruto Island, Mozambique)

DIAGNOSIS. Dorsal fins III + XIII + 10–11; anal fin I, 18–20 (usually 19–20 rays); pectoral fins 15–16: 2, 6, 7 or 2, 7, 7. Lateral line 24–30 (usually 27–28, rarely 24 or 30) tubed scales, ending below middle of third dorsal fin; total lateral scales 37–38; transverse scales 9/7. Vertebrae 11 + 23–25 (24; 1 of 17 with 23, and 1 with 25); 1 free pterygiophore between second and third dorsal fins. Mandibular pores 4 + 1 + 4 (rarely 3 + 1 + 3) (Fig. 9c) Head narrow and elongated, its length 3.1–3.6 (3.4) in SL; eye 2.6–3.1 (2.9), maxilla 2.1–2.5 (2.2) in head length; interorbital width about 2/3 pupil diameter.

Nape scaled, but scales not to base of first dorsal fin anteriorly; 2 or 3 rows of scales on base of caudal fin; scales on underside of caudal peduncle; scales do not extend to base of anal fin anteriorly. Pelvic-fin rays united by membrane for two-thirds length of shorter, half length of longer ray, longest ray nearly reaching vent. Origin of first dorsal fin over posterior margin of preopercle, fin of males triangular with first spine taller than second dorsal fin, in females slightly shorter than second, in both sexes first two spines closer together than second and third spines. Maxilla reaches past vertical through anterior margin of pupil. Inner margin of upper lip crenulate; lower labial folds narrow (Fig. 9c). Broad patch of teeth in both jaws in front, with single row of enlarged teeth on outer margin, continuing to side of jaw. Orbital cirrus simple and pointed, in length about half of pupil diameter.

Live colour. (Based on freshly preserved material.) Males dark pink with three orange blotches at base of second dorsal fin and three at base of third dorsal fin. Dark pink blotches along midside and eight dark pink spots along anal-fin base; belly white. Head slate-grey to black below eye, with orange spots above. Membrane between first two dorsal-fin spines orange and black, remainder of first dorsal fin black (see preserved colour below); second dorsal fin black and orange basally; third dorsal fin similar but paler. Anal fin black with orange along rays corresponding to colour on body. Caudal fin pinkish with orange at base of rays. Pectoral fins with orange on middle and upper rays; pelvic fins without colour. Females very similar to males but lack the black on the head and median fins, and have a narrow dark bar across the caudal peduncle, at the base of the caudal fin.

Colour in alcohol. Males: body with irregular groups of melanophores suggestive of banding above lateral midline; cluster of few melanophores around vent.

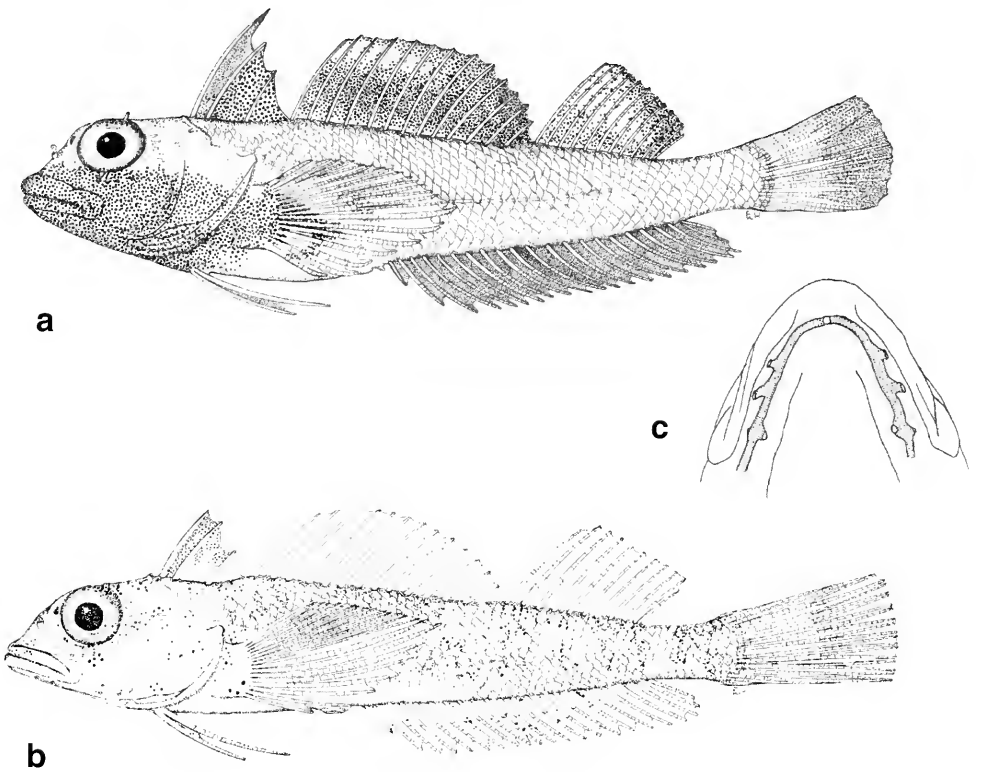


Fig. 9. *Helcogramma microstigma*. **a**, holotype, SAIAB 73754, male, 29.0 mm SL; **b**, paratype, SAIAB 73753, female, 27.9 mm SL, both from Bazaruto Island, Mozambique; **c**, mandibular pores.

Head below eyes with dense and evenly spread melanophores extending to base of pectoral-fin rays and along throat to base of pelvic fins. Top of head with few, small melanophores, interorbital area immaculate. First dorsal fin evenly marked with densely packed melanophores, those on membrane between first two spines very small; basal half of second dorsal fin black, followed by a paler band and with a black band along margin; third dorsal fin similar. Distal third of caudal fin spotted with melanophores. Anal fin black with many small and evenly spread melanophores on both rays and membranes. Pelvic-fin membrane of large males with cluster of small melanophores in middle. Pectoral-fin membranes with some spotting.

Females with banding on body more obvious, patches of melanophores extending to below midline. Large individuals with narrow dark bar across caudal peduncle at base of caudal fin. Scattered melanophores on head and a small cluster on lower pectoral-fin base. First dorsal fin membrane between first two spines as for males, with many micro-melanophores, but not as dark.

DISTRIBUTION (Fig. 1). The species is known from the Comoro Islands, northern Madagascar, and Bazaruto and Inhaca Islands, Mozambique.

COMPARISONS. *H. microstigma* occurs sympatrically with *H. alkamr*, *H. ememes* in the Comoro islands and with *H. fuscopinna* in the Comoro Islands and along the east coast of Africa and northern Madagascar. The species can be distinguished from all of these by its tall first dorsal fin with micro-melanophores on the membrane between the first two spines.

REMARKS. *Helcogramma microstigma* is a member of the *H. steinitzi* species group that also includes *H. rosea* (see below), which share a tall first dorsal fin with the first two spines set close together and the membrane between them with micro-melanophores. The three species occur in geographically separate areas (see Holleman 2006).

NOTE. The key and illustration (Fig. 1) given in Holleman 2006 are incorrect. In the key the presence or absence of micromelanophores on the saddles at the end of the second and third dorsal fins was inverted and should read as in the key above (p. 53). Fig. 1 shows an orbital cirrus of about half eye diameter instead of about half pupil diameter, as shown in Fig. 9 above.

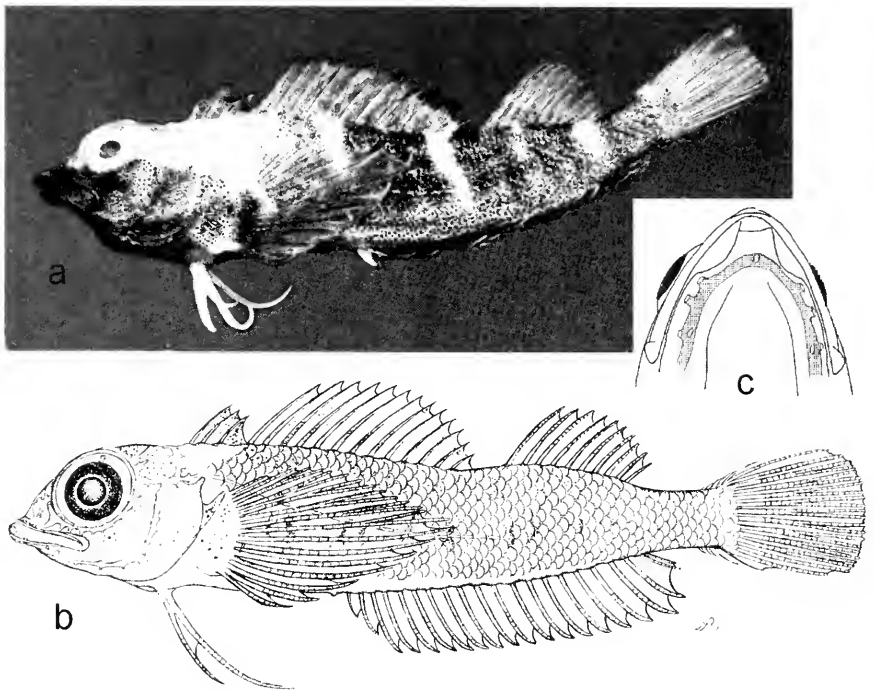


Fig. 10. *Helcogramma obtusirostre*. **a**, male, 37.9 mm SL; **b**, HUJ 64/36b, female, 21.9 mm SL, Elat, Red Sea (a & b from Clark, 1979); **c**, mandibular pores.

***Helcogramma obtusirostre* (Klunzinger)**
Figs. 1 & 10, Plate 2

Tripterygium obtusirostre Klunzinger 1871: 498 (Red Sea).
Helcogramma obtusirostre Clark 1979: 85, figs. 3e, 7 & plate 1; Holleman in: Smith & Heemstra 1986: 757; Randall 1995: 309, fig. 872.
Helcogramma obtusirostris Hansen 1986: 341 (in part: Red Sea – see Note on nomenclature);
Helcogramma trigloides (non Bleeker) Marshall 1952: 242 (Gulf of Aqaba)
non *Helcogramma shinglensis* Lal Mohan 1971: 219, fig. 1 (Gulf of Mannar, India)
non *Helcogramma ascensionis* Lubbock 1980: 294, fig. 2 (Ascension Island, S Atlantic)

DIAGNOSIS. Dorsal fins III + XII–XIII + 9–10 (rarely with XII spines or 9 rays); anal fin I, 18–19 (usually 19); pectoral fins 16: usually 2, 7, 7. Lateral line 20–23 (usually 21–22) tubed scales, ending below junction of second and third dorsal fins; total lateral scales 36–38 (usually 37–38); transverse scales 7/5. Vertebrae 10 + 25–26; 1 free pterygiophore between second and third dorsal fins. Mandibular pores 4 + 1 + 4 (Fig. 10c). Head length 3.3–3.7 (3.5) in SL; eye 2.6–3.2 (2.8), maxilla 2.2–2.6 (2.4) in head length.

Nape and belly naked; scales do not extend to bases of first dorsal and anterior of anal fins; 2 rows of scales on base of caudal fin. Pelvic-fin rays united by membrane for half shorter ray, longest ray reaching vent. First dorsal fin half height of second. Maxilla reaches vertical through centre of pupil; orbital cirrus small and simple.

Live colour. (From colour photograph by J. E. Randall.) Body of males mottled greenish with darker interconnecting areas, with 4 narrow, pale saddle marks extending from base of dorsal fins to midline, 2 below second dorsal fin, 2 below third dorsal fin; series of paler spots along midline; dorso-anteriorly suffused with dull red; belly pink. Head dark, black below eye and to branchiostegal membrane; bright blue stripe extends from lower lip across cheek, broadly edged with black above and below. Pectoral-fin base with red spot above and below, the lower one with blue above and anterior; pelvic fins dark pink proximally; first dorsal fin dusky with some orange, darkest on the margin, and with small black spot at base of membrane connecting first and second dorsal fins; second dorsal fin dusky with dull orange band basally; third dorsal fin dusky; caudal fin dusky; anal fin dark, with an even cover of melanophores.

Females dull green, the dark areas forming a zig-zag pattern down the body, on a pale green background; body pale ventrally. Head dorsally dark green, ventrally pale; median fins with light sprinkling of melanophores, first dorsal fin with small black spots as in males, base third dorsal and entire anal fins white.

Colour in alcohol.
Body of adult males heavily pigmented with melanophores, except for nape and area above pectoral-fin base and 3 or 4 pale, narrow saddles extending from dorsum to midline or below. Head below level of eye, including lips, heavily stippled with melanophores, which extends to pelvic-fin base and belly. Pectoral-fin base with melanophores except for clear area at lower edge. Charcoal to black half-moon of melanophores at base of pectoral-fin rays; lower rays dusky. Dorsal fins dusky, third the least dark; anal fin dusky to black; caudal fin dusky, pelvic fins without pigment.

Females largely unpigmented, except for scattered melanophores dorsally on body, in small clusters along midside, on first and second dorsal fins and on the pectoral fin base.

Distribution (Fig. 1). *Helcogramma obtusirostre* is known from the Red Sea, Yemen and Oman.

Comparisons. This species occurs with only one other species of the genus, *H. steinitzi*, which is generally larger and red in colour, has a first dorsal fin as tall as the second (half the height in *H. obtusirostre*, and mature males are black) and has 4 + 1 + 4 mandibular pores vs 3 + 1-2 + 3 for *H. steinitzi*. *H. obtusirostre* also has a blue stripe from the corner of the mouth onto the preopercle, which is absent in *H. steinitzi*.

Remarks. Hansen (1986) synonymised several species with *H. obtusirostre* as they are generally impossible to separate on fin and scale counts, including *H. ascensionis*, *H. shinglensis* and *H. trigloides*. She also included material from southern Africa as *H. obtusirostre*, following Holleman (1978, unpublished data). Close examination of specimens and photographs of *H. ascensionis* determined that it was not conspecific with the southern African species-described as new below-and that the southern African species was not conspecific with *H. obtusirostre*. There are colour differences between the three species. However, they also share a blue stripe that runs from the corner of the mouth onto the preopercle. These three species belong to a species complex that includes *H. ellioti*, *H. trigloides* and *H. fuscipectoris*, and possibly additional species from the Western Pacific. *H. shinglensis* differs from *H. obtusirostre* in mandibular pore pattern and is here recognised as a valid species, together with *H. ascensionis* (see also under *H. shinglensis*).

Material examined. **Red Sea**: HUJ 9188 (10: 21.0-25.9 mm) and HUJ 9189 (10: 17.2-24.3 mm), Dahlak Archipelago.

Helcogramma rharhabe sp. nov.
Figs. 1 &11; Plate 2

Holotype: SAIAB 70740, 35.6 mm SL male; Sheffield Beach, KwaZulu-Natal, South Africa; open gully with corralines, 0-3 m depth; collected R. Winterbottom & R. E. Stobbs, 4 September 1974; field number RW 74-22.

Paratypes. **South Africa**: MNHN 2006-1693 (6: 31.0-37.4 mm); ROM 73759 (3: 34.2-32.5 mm); SAIAB 55017 (17: 25.9-36.9 mm); USNM 375019 (3: 30.5-31.6 mm), all ex SAIAB 32404 from Coffee Bay, Eastern Cape; AMS 42930-001 (6: 22.4-34.8 mm); BMNH 2004.1 6.1-6 (6: 27.5-36.0 mm); BMNH 2004.1.6.10-16 (7: 19.4-33.0 mm); ROM 73758 (6: 24.5-36.9 mm); SAIAB 70754 (18: 17.5-35.0 mm); WAM P32852-001 (ex SAIAB 32407) (6: 24.5-36.9 mm); USNM 375017 (6: 21.8-36.7 mm); all same collection as Holotype; ROM 73760 (5: 22.6-33.0 mm); SAIAB 70752 (25: 19.0-32.0 mm); USNM 375018 (5: 21.3-33.8 mm), Sodwana Bay, KwaZulu-Natal. **Mozambique**: SAIAB 70746 (20: 13.8-31.0 mm), Punto Milibangalala; SAIAB 7438 (19.6 & 27.2 mm), Ilha do Bazaruto.

Diagnosis. A medium to large species of *Helcogramma* with a naked nape, 5 + 1 + 5 mandibular pores, males with a bright blue streak from corner of mouth onto

Table 6. Counts for *H. rharhabe* from different localities.

Locality	D2 spines			D3 rays		Anal-fin rays				Lateral line scales										
	12	13	14	10	11	17	18	19	20	20	21	22	23	24	25	26	27	28	Mean	Mode
Transkei - Coffee Bay (31°59'S) n=39	6	31	3	22	16		3	33	3				4	9	4	7	5	3	25	24
Mid-KZN - Chaka's Rocks (29°30'S) n=22		20	1	14	7		2	20		1	1	2	4	5	3	2	2	2	24	24
N. KZN - Six Mile Reef (27°38'S) n=20		16	4	13	7	1	1	18				5	7	2	2	1	1		23	23
S. Moz. - Ponta do Ouro (26°51'S) n=3	1		2		3			2	1				1		1					
- Ponta Milibangalala (26°25'S) n=20	1	16	3	15	5			20			1	4	7	4	2				23	23
- Inhaca Island (26°00'S) n=17		15	2	11	6		2	15			2	3	7	2		2			23	23
N. Mozambique - Zavora (24°25'S) n=11	1	9	1	6	5		2	7	2		2	3	2			1*			23	22
- Bazaruto (21°40'S) n=3		3		2	1			3				2		1					23	22

* Counted as 24+blank+1=26
KZN = KwaZulu-Natal

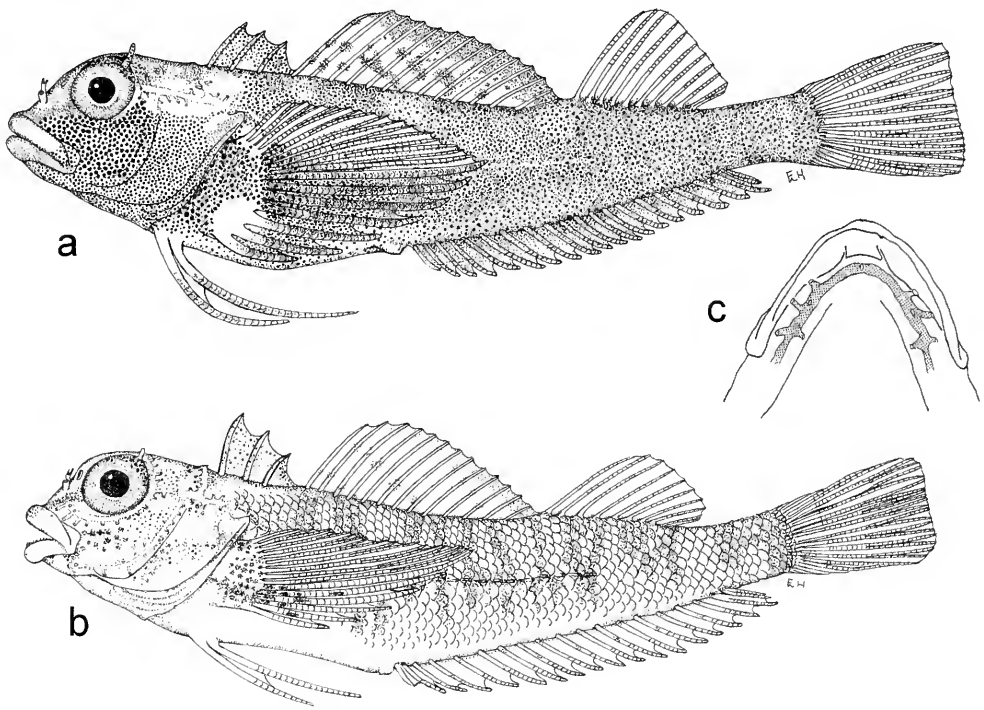


Fig. 11. *Helcogramma rharhabe*. **a**, holotype, SAIAB 70740, male 35.6 mm SL, Sheffield Beach, Kwazulu–Natal, South Africa; **b**, paratype, SAIAB 55017, female, Coffee Bay, E. Cape, South Africa; **c**, mandibular pores.

pre-opercle and crimson marks either side on upper lip, black in the centre.

DESCRIPTION. Dorsal fins III + XII–XIV + 10–11 (usually III + XIII + 10); anal fin I, 19 (rarely with 18 or 20 rays); pectoral fins 15–16: usually 1, 8, 7. Lateral line 21–31 tubed scales (mean dependent on locality – see Table 5), usually ending below junction of second and third dorsal fins; total lateral scales 37–38 (usually 38). Vertebrae 10 + 24–25; 1 free pterygiophore between second and third dorsal fins. Mandibular pores 5 + 1 + 5 (Fig. 11c). Head length 3.3–3.7 in SL; eye 2.6–3.2, maxilla 2.2–2.6 in head length–see Table 6 for geographic variation.

Nape and belly naked; scales do not extend to bases of first dorsal and anterior of anal fins; 2 rows of scales on base of caudal fin. Pelvic-fin rays united by membrane for 1/2 length of the shorter ray, longest ray reaching anterior margin of vent or mid-vent. First dorsal fin half height of second. Maxilla reaches vertical through anterior margin of pupil; orbital cirrus small and simple.

Live colour. Entire body of mature males heavily and evenly spotted with black and some dark red, except for 4 pale streaks extending from base of dorsal fin to latreal midline, the first below middle of second dorsal fin, second below junction of second and third dorsal fins, third below middle of third dorsal fin and the last streak below end of third dorsal fin, and 6 or 7 bright, silvery-white spots just below midline. The saddle marks and spots below the midline may become entirely obscured in very heavily pigmented specimens. Belly pale with fine melanophores. Head below eye black, with bright blue-white streak extending from lower lip, through corner of mouth onto preopercle; upper lip with crimson red patch on either side, black in the centre and blue at corner of mouth; area above upper lip and interorbital green; top of head reddish to black, with many small melanophores. Throat blue and black. First dorsal fin with gold and black spots on membrane between first two spines and along margin of other membranes; second dorsal fin hyaline with brown to black margin and dark red, black and white scattered irregularly on the membranes and spines; third dorsal fin with red along edges of rays and a grey margin; caudal fin mostly without pigment, some red and black on lowermost 2–3 rays. Anal fin evenly covered with red and black spots; base of pelvic fins crimson; pectoral fin base with red spots above and below at base and with bright blue above and anterior to lower spot, and black half-moon to triangular blotch, apex posterior on base of cental rays; base of upper 3–4 rays red, of lower 2 rays with crimson spot; other rays dusky.

Females pale green dorsally, some scales edged in brown, forming pairs of semi-bars that are extensions of bars on dorsal fins. Body below midline transparent with black semi-bars with interspersed white spots. Head brown-green above, whitish below, with

scattered melanophores. Dorsal fins with alternating irregular pale and dark bars, the colour confined to the elements. Caudal fin transparent with whitish band at base of rays; anal fin with some melanophores along the edges of the rays. Pelvic fins whitish; pectoral fins with irregular dark brown, white and greenish bands.

Colour in alcohol. All colour fades; relatively newly preserved males have dark brown bodies with an overlay of many melanophores, with 4 pale streaks and white spots below lateral line. Head with unpigmented spots on either side of upper lip and otherwise covered variously with scattered melanophores above eye and dense spotting below eyes, throat and to pelvic-fin base. An oval area around base and proximal half of pelvic fins with no pigment, distal half with fine spotting. Dorsal fins with margin of small melanophores and irregularly banded with brown; third dorsal fin without pigment; anal fin covered with brown and black spots. In heavily pigmented specimens the first two dorsal fins are entirely covered with brown and black spots. Pectoral-fin bases with clear semi-circles above and below, rays irregularly banded with brown and black spots. In time the brown and white pigments also disappear.

Females retain very little colour, initially only the white spots below the midline and eventually only scattered melanophores, which may give some suggestion of irregular half-bars.

Etymology. In the Eastern Cape, South Africa, the species is sometimes known as "hotlips" on account of its crimson upper lip. It is, however, named "rharhabe", after the eldest son of Phalo, paramount chief of amaXhosa. In c. 1750 Rharhabe and his father quelled an uprising by Rharhabe's half-brother, Gcaleka, and subsequently lead a break-away group which Rharhabe ruled as paramount chief from 1775 to 1787 (Owen, 1994). The name is to be treated as a noun in apposition.

Distribution (Fig. 1). *Helcogramma rharhabe* is common to abundant in tide pools and the shallow sub-tidal zone from East London, South Africa (33° S) to Ilha do Bazaruto, Mozambique (21°40′ S). In KwaZulu-Natal, South Africa, as many as 1 000 individuals have been collected from a single, large pool. Two specimens, females, from Shimoni, Kenya, (4°37′ S) may be referable to the species, but are in poor condition and, until additional material is available, the northernmost limit is considered to be Bazaruto.

Comparisons. *H. rharhabe* occurs together with *H. fuscopinna* throughout most of its range, and with *H. alkamr* along the coast of Mozambique. Male *H. rharhabe* have partially red lips and a blue stripe from the corner of the mouth onto the preopercle, whereas the distinctive blue stripe of male *H. fuscopinna* runs from the middle of the upper lip, below the eye and onto the opercle. These two species can also be separated by second dorsal-fin count: a norm of 13 spines vs 14 for *H. fuscopinna*. Male *H. rharhabe* can be distinguised from *H. alkamr* by body colour, black vs brown for the latter species.

Non-type material examined. **Mozambique**: SAIAB 7434 (3: 24.2–33.8 mm); SAIAB 7441 (3: 30.8–35.1 mm); SAIAB 7443 (10: 24.6–34.5 mm), Inhaca Island; SAIAB 7433 (32.4 mm), Maputo Bay; SAIAB 50681 (6: 13.8–28.0 mm), Ponta do Ouro. **South Africa**: SAIAB 32431 (20: 21.0–33.0 mm), Six Mile Reef, KwaZulu-Natal; SAIAB 32393 (28: 18.9–37.2 mm), Chaka's Rocks, KwaZulu-Natal; SAIAB 32394 (23: 28.6–39.1 mm); SAIAB 55017 (16: 25.9–36.9 mm), Coffee Bay, Eastern Cape.

Helcogramma rosea Holleman
Figs. 1 & 12, Plate 2

Helcogramma rosea Holleman 2006: 95, figs. 3–5 (Phuket, Thailand)

Diagnosis. Dorsal fins III + XIII + 11 (rarely 10 rays); anal fin I, 18–20 (rarely 18, usually 20 rays); pectoral-fin rays 16: usually 2, 7, 7. Lateral-line tubed scales 23–29 (usually 25–27); total lateral scales 36–38 (usually 37). Vertebrae 11 + 24–26 (25; 1 of 32 with 26), 0 or 1 free pterygiophores between second and third dorsal fins. Mandibular pores 3–4 + 1 + 3–4 (Fig. 12c); pore on inside of ramus small and absent in about 60% of specimens examined). Head length 3.1–4.0 [3.3] in SL; eye 2.8–3.4 [3.1], maxilla 2.0–2.3 [2.2], snout 3.1–3.9 [3.5], in head length; head profile fairly blunt, 56–62° [60°].

Nape scaled, but scales do not extend to base of first dorsal fin anteriorly; 2–3 rows of scales on base of caudal fin; scales on underside of caudal peduncle; scales do not extend to base of anal fin anteriorly. Pelvic-fin rays united by membrane for half length of longer ray, longer ray extends nearly to vent in males, about 80% of distance in females. Origin of first dorsal fin over posterior margin of preopercle, fin of males males triangular, with first spine equal in height to second dorsal fin, in females first 2 dorsal-fin spines subequal, and fin about 80% height of second dorsal fin; first two spines closer together than half distance between second and third spines. Maxilla reaches vertical through centre of pupil. Broad patch of teeth in front of both jaws, narrowing to single row on either side; vomer and palatines with patches of teeth. Orbital cirrus small, triangular and rounded, a little longer than wide.

Live colour: (from photographs by R. Winterbottom). Males with red body and three small, yellow saddles, first below anterior of second dorsal fin, second below

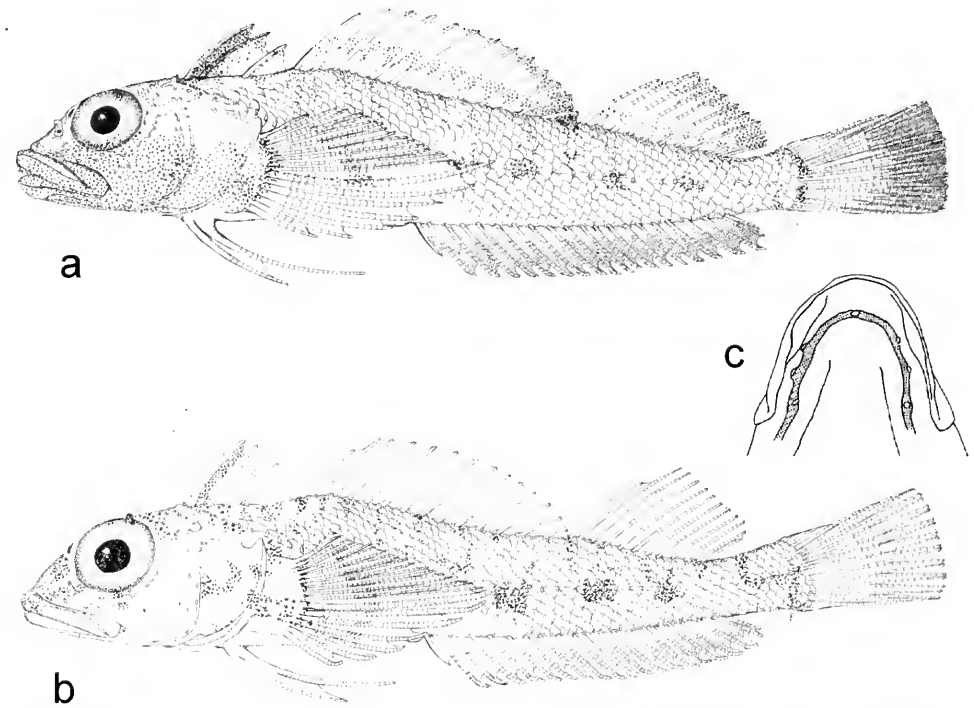


Fig. 12. *Helcogramma rosea*. **a**, holotype, ROM 76679, male, 34.4 mm SL; **b**, paratype, ROM 76680, female, 27.6 mm SL, both from Phuket, Thailand; **c**, mandibular pores.

end of second dorsal fin and third below end of third dorsal fin, with line of yellow dots and dark brown dashes along lateral line and narrow dark bar across the peduncle; belly spotted red. Head reddish above, dark brown behind eyes and to posterior edge of opercle, pale with dark spots below eyes, to pelvic-fin base; dark-brown, oblique bar from lower margin of eye with pale blue anterior to and below eye, and bright yellow spot immediately behind eye. Iris red with yellow spots, nasals and centre of upper lip brown. First dorsal fin pale with brown and red spots; second with red spots basally and brownish margin; third with red spots basally and red and black along margin. Caudal fin mostly deep pink with small black spots antero-ventrally. Anal fin spotted with red and black, the black darkest along margin. Pectoral-fin base brown with two pale blue spots at centre and at lower edge, fin entirely red with three pale "bars", colour on rays only. Pelvic fins pale, red basally.

Females with light cream body, greenish above lateral line, with series of chocolate brown blotches along lateral line, pairs of brown "saddle" marks, three below second dorsal fin, two below third dorsal fin and one on peduncle, last half-pair forming narrow bar across peduncle; anal fin with seven subcutaneous, brown blotches along base. Head, nasals, upper lip, preopercle and opercle mottled brown and cream, pale cream below eye with some brown marks. First dorsal fin with brown, second and third with brown on spines and rays roughly corresponding to "saddles" on dorsum. Caudal fin pale with a little colour along the rays; anal fin with spots along margin, colour on rays only.

Colour in alcohol: Males with pale body with clusters of melanophores along midline, last forming a narrow bar across caudal peduncle; scattered melanophores above midline, with groups of micro-melanophores where yellow saddles are in life; cluster of small melanophores adjacent and posterior to genital papillae. Head with scattered melanophores on top and in interorbital area; closely and evenly spaced melanophores below eye, which continue onto the anterior of belly, either side of pelvic-fin base, and onto pectoral-fin base, where colour is darkest at base of central rays. First dorsal fin with closely spaced micro-melanophores on membrane between first two spines, other membranes with few large spots; second dorsal fin with broad band of melanophores along middle of fin narrow band along margin; third similar to second, but lighter. Anal fin with many small melanophores on membranes and rays, darker along the margin in smaller specimens, evenly spread across entire fin in large specimens. Pectoral fins with rows of micro-melanophores on some rays, suggestive of two bars across fin.

Mature females are very similar in colour to males, melanophores on dorsum suggestive of short bars with clusters along midline and series of subcutaneous spots along base of anal fin. Head with few melanophores, most notably clusters on upper lip either side of symphysis, and semicircular cluster,

open anteriorly, on opercle. First dorsal fin as in males; second and third with small melanophores on elements, continuous with short bars on body. Pectoral-fin base with two clusters of melanophores, one dorsally and one ventrally on base.

Distribution (Fig. 1). The species is known from Sri Lanka and the Andaman Sea.

Comparisons. *Helcogramma rosea* occurs sympatrically with several other *Helcogramma* species at Sri Lanka, and can be distinguished from them by its tall first dorsal fin with the close-set first two dorsal-fin spines with micro-melanophores on the membrane between them.

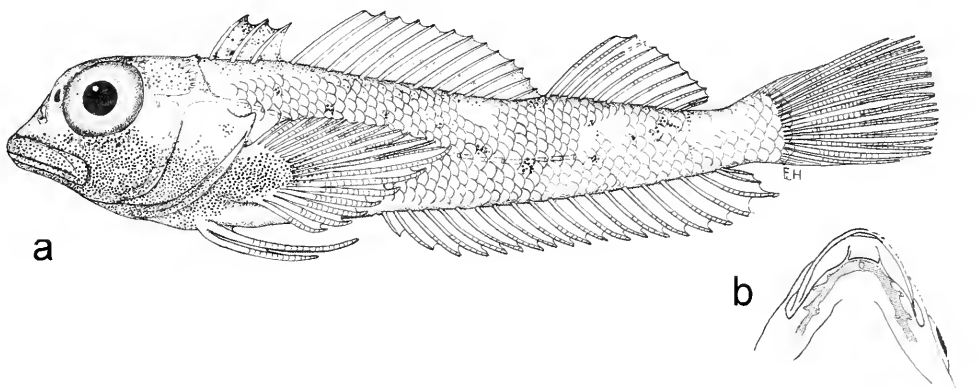


Fig. 13. *Helcogramma serendip*. **a**, holotype, SAIAB 73755, male, 21.8 mm SL, Trincomalee, Sri Lanka; **b**, mandibular pores.

***Helcogramma serendip* sp. nov.**
Figs. 1 & 13

Holotype: SAIAB 73755, male, 21.8 mm SL; near Fort Frederick, Trincomalee, Sri Lanka; rocky bottom (?); collected Hans Bath, 20 May 1982.

Paratypes. **Sri Lanka**: SAIAB 73756 (12: 17.3–23.2 mm), same collection as Holotype; USNM 385565 (23.5 & 24.2 mm), and USNM 228981 (3: 15.9–22.8 mm) Trincomalee; USNM 385567 (5: 17.6–19.5 mm), and USNM 228977 (5: 19.2–24.8 mm), Koddiyar Pattu.

Diagnosis. A small species of *Helcogramma*, less than 25 mm SL, with a low first dorsal fin, 4 + 1 + 4 mandibular pores and minute serrations on posterior margin of orbit and edges of occipital sensory canals.

Description. Dorsal fins III + XIII + 10; anal fin I, 18–19 (usually 19 rays); pectoral fins 16: usually 2, 7, 7. Lateral line 20–22 (mode 21) tubed scales, ending below the junction of the second and third dorsal fins; total lateral scales 36–39 (usually 38). Vertebrae 10 + 25 (1 of 12 with 25); 1 free pterygiophore between second and third dorsal fins. Mandibular pores 4 + 1 + 4 (Fig. 13b) Head length 3.3–3.9 (3.6) in SL; eye 2.5–3.0 (2.8), maxilla 2.1–2.8 (2.4) in head length; head quite blunt—72–76° (74°).

Nape naked, but with patches of scales above first few lateral-line scales; two rows of scales on base of caudal fin; scales do not extend to base of anal fin anteriorly; no scales on underside of caudal peduncle. Posterior margin of eye with small serrations on edge of frontal bones; edges of sensory canals extending back from the one immediately behind the eye with fringe of minute serrations. First dorsal fin less than half height second dorsal fin. Pelvic-fin rays united by membrane for length of shorter, half length of longer ray, longest ray reaching about $^{4}/_{5}$ ths of distance to vent. Lower labial folds relatively large (Fig. 13C). Broad patch of teeth in front of both jaws, single row at sides, with row of enlarged teeth inside middle of upper jaw, both outside and inside middle of lower jaw. Maxilla reaches vertical through anterior of pupil. Small, pointed orbital cirrus present. Interorbital width about equal to pupil diameter.

Live colour. Not known
Colour in alcohol. Males with evenly-spaced melanophores from level of upper lip, below eyes and onto opercle and pectoral-fin base, where they form a triangle, apex posterior; pigment stops abruptly between isthmus and base of pelvic fin. Top of head and interorbital with small melanophores. Body with scattered melanophores above lateral midline and with 7–8 clusters on midline, from below pectoral fin to caudal peduncle, the darkest cluster anteriorly. First and second dorsal fins with black spots along margin; third dorsal fin unpigmented; anal fin with melanophores on membranes in band along middle of fin. Caudal and pelvic fins unpigmented.

Females with 7 'H'-bars along on body along midline, 1–4 below second dorsal fin, 5 and 6 below third fin and last across peduncle. Head, opercle and

pectoral-fin base with scattered melanophores; cluster of melanophores below eye and a stripe from corner of mouth onto upper lip. First dorsal fin with dark margin, other fins without pigment.

DISTRIBUTION (Fig. 1). The species is currently known only from Sri Lanka.

Etymology. The name is taken from the old Arabic name for Sri Lanka, 'Sarandib', or 'Serendip' in English, currently the only known locality of this species. It is also given in recognition of the way in which many new species are discovered—serendipitously. The specimens were amongst several lots collected by Hans Bath in 1982 and which he donated to SAIAB. The epithet is used as a noun in apposition.

COMPARISONS. See under *H. ellioti*.

REMARKS. *H. serendip* is very similar to *H. chica* Rosenblatt (1960), which is recorded from the Christmas, Cocos-Keeling Islands and eastwards to the Society Islands. *H. chica* lacks the orbital cirrus present in *H. serendip*. The mandibular pore pattern for *H. chica* is 3-4 + 1 + 3-4, while for *H. serendip* it is 4 + 1 + 4. The facial pigment of *H. chica* males as described by Hansen (1986: 331) and Fricke (1997: 423) appears identical to that of *H. serendip*, ending abruptly between the isthmus and the base of the ventral fins. A further similarity between *H. chica* and *H. serendip* is the "feeble development of spination along the path of the mucous canals of the frontals ....." Schultz, 1960: 296), which I have described as a "fringe of minute serrations".

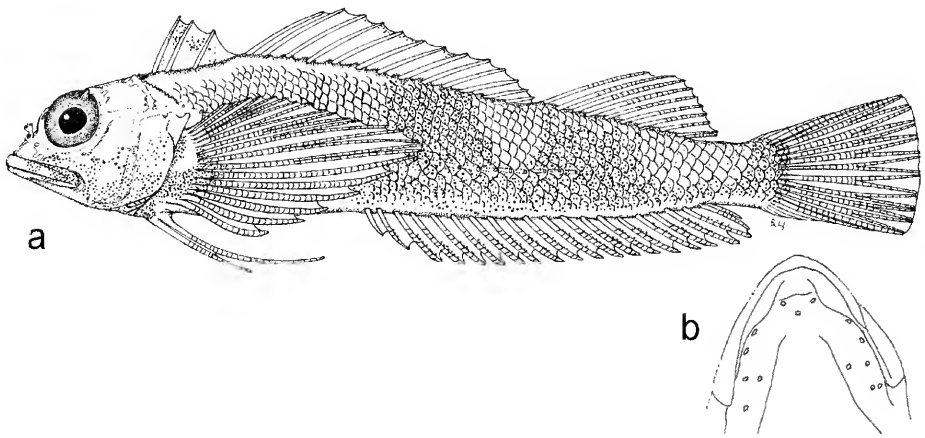


Fig. 14. *Helcogramma shinglensis*. **a**, male, SAIAB 30429, male, 26.9 mm SL, Trincomalee, Sri Lanka **b**, mandibular pores.

Helcogramma shinglensis Lal Mohan
Figs. 1 & 14, Plate 2

Helcogramma shinglensis Lal Mohan 1971: 219, fig. 1 (Gulf of Mannar, India).
Helcogramma obtusirostris Hansen 1986: 341

DIAGNOSIS (The counts for Lal Mohan's four type specimens are given in squared parenthesis). Dorsal fins III + XIII + 10 [III + XII-XIII + 9]; anal fin I, 19-20 [I, 20]; pectoral fins 15-16 [15]: usually 1 + 8 + 7. Lateral line 21-24 [20-22] tubed scales, ending below the junction of the second and third dorsal fins; total lateral scales 37-38; transverse scales 10/5 [11/4]. Vertebrae 10 + 24-25; 1 free pterygiophore between second and third dorsal fins. Mandibular pores 4-6 + 3 + 4-6 (Fig. 14b). Head length 3.5-3.6 in SL; eye 2.7-2.8, maxilla 2.2-2.4 in head length.

Nape and belly naked; scales do not extend to bases of first dorsal and anterior of anal fins; scales on ventral surface of peduncle absent; 2 rows of scales on base of caudal fin. Pelvic-fin rays united by membrane for half the length of the shorter ray, longest ray reaching vent. First dorsal fin half height of second. Maxilla reaches vertical through centre of pupil; orbital cirrus small and pointed.

Live colour. Lal Mohan records that *H. shinglensis* and *H. ellioti* are very similar in colour. He describes the colour of males as follows: "Head with black pigments ventrally, body and orbits red, lower half of pectoral (base?) black, dorsal fin hyaline, nape to middle of second dorsal fin with red pigments, a vertical band at the origin of the second dorsal fin, another at the end of the third dorsal fin, caudal fin hyaline with greenish taint ventrally, pelvic fins red. In formalin colour fades, body light greenish interrupted with brown pigments, pectoral peduncle with blue blotch." (Ibid. p. 222). There are no known colour photographs of the species.

Colour in alcohol. Body of males posteriorly dark brown with many small, dark brown spots in coloured areas, anteriorly light brown with spots, with two prominent unpigmented "saddles", one below end of second dorsal fin, the second below end of third dorsal fin, extending across body; belly pale. Head below eye dark brown with darker spots, colour to pelvic-fin base, and onto pectoral-fin base; branchiostegal membranes dark brown; head above lower level of eye pale with small, light brown spots. First and second dorsal fins with spotted margins; third immaculate; anal fin with brown spots on distal half, on entire fin in dark males. Lower rays of caudal fin with some colour at base of rays. Pectoral-fin base with immaculate area above and below brown line, brown line confluent with very dark brown triangular mark at base of middle rays, apex posterior; lower, undivided rays with brown in dark males; pelvic fins without colour.

Body of females with scattered dark brown spots on upper half and light brown blotches that extend to below the lateral line, and light brown band with some dark spots across peduncle at caudal-fin base. Top of head with minute dark brown spots; opercle with dark brown spots and cluster below eye and on either side of centre of upper lip, spots extending to anterior rim of eye. First dorsal fin with dark brown spots on membranes; second with narrow band of dark brown spots along margin; third dorsal, caudal and anal fins without pigment. Pectoral-fin base with light brown blotches and a small cluster of dark brown spots at base of rays 8-10, with smaller spots on lower rays suggestive of banding.

Distribution (Fig. 1). The species has been recorded only from Sri Lanka and the Gulf of Mannar.

Comparisons. In southeast Indian waters *H. shinglensis* occurs sympatrically with four other *Helcogramma* species: *H.billi*, *H. rosea*, *H. serendip* and *H. ellioti*. It can be distinguished from the first three species by having 3 symphyseal mandibular pores vs only one, and from *H. ellioti* by fewer tubed lateral-line scales-21-24 vs 33-37 for *H. ellioti*.

Remarks. Hansen examined the types of *Helcogramma shinglensis* Lal Mohan (1971: 219), as well as specimens of *Helcogramma ascensionis* Lubbock (1980: 294) and synonymised these two species with *H. obtusirostre*. It is curious that, having found that the mandibular patterns of *Helcogramma* species were consistent for a species, she should have synonymised *H. shinglensis* (having examined the types) with *H. obtusirostre* when the former has a pore pattern of 4 + 3 + 4 cf. 4 + 1 + 4 for *H. obtusirostre*. I have not seen all the Indian Ocean specimens that Hansen looked at, but the specimens from the Seychelles, Comore Islands, Tanzania and St Brandon Shoals have all been identified as *H. alkamr*.

Material examined. **Sri Lanka**: SAIAB 30429 (26.9 mm); USNM 222306 (24.1 & 24.5 mm); USNM 222375 (26.9 mm); USNM 222379 (8: 24.1-21.0 mm), Trincomalee; USNM 228976 (4: 18.5-22.2 mm), and USNM 385566 (3: 15.9-22.8 mm), Kodiyar Pattu.

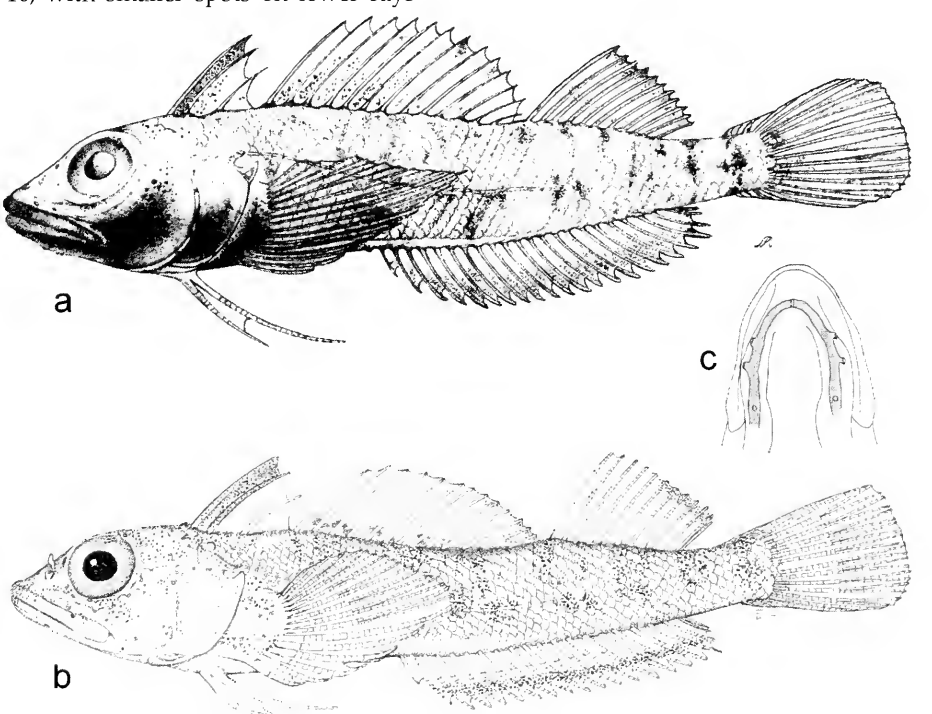


Fig. 15. *Helcogramma steinitzi*. **a**, paratype, ex USNM 205824 male, 36.5 mm SL (from Clark 1979) (first dorsal fin constructed from another specimen); **b**, paratype, ex USNM 205833, female, 29.5 mm SL, both from Aqaba, Red Sea; **c**, mandibular pores.

***Helcogramma steinitzi* Clark**
Figs. 1 & 15; Plate 2

Helcogramma steinitzi Clark 1980: 88, fig. 8, Pl. II–V (Red Sea); Hansen 1986: 347; Randall 1995: 310.

DIAGNOSIS (partially from Clark 1980 and Randall 1995). Dorsal fins III + XII–XIV + 10–12 (usually III + XIII + 10–11); anal fin I, 19–21 (usually 20); pectoral fins usually 15–17 (recorded by Clark and Randall; usually 16: 2, 7, 7). Lateral line 21–27 tubed scales, ending below first five rays of third dorsal fin; total lateral scales 38–40 (37–41, from Clark). Vertebrae: 11 + 24–25; 1 free pterygiophore between second and third dorsal fins. Mandibular pores 3 + 1 + 3 (Fig. 15c). Head length 3.0–3.5 in SL; eye 3.0–3.4, maxilla 2.0–2.1 in head length.

A large species, reaching nearly 60 mm SL. Nape scaled, belly naked, scales do not extend to base of first dorsal or anal fins; 1 or 2 rows of scales at base of caudal fin. Pelvic-fin rays united by membrane for half length of shorter ray, longer ray reaching vent. Origin of first dorsal fin over posterior margin of preopercle, fin triangular, in males first spine fin about as long as longest spine of second dorsal fin, in females a little shorter; first two spines set close together. Mouth large, maxilla reaching vertical through posterior of pupil; orbital cirrus minute.

Live colour (based on Randall 1995). Body of males dark red above lateral line, many scales outlined in black, paler red below lateral line, with white flecks and indistinct black markings forming a reticulated pattern, and with 8 dark blotches interspersed with white blotches along mid-side below lateral line; belly white. Head deep above lower level of eye dark red, below bluish-grey with many small melanophores, and a bluish streak below eye. First dorsal fin with red and black spots; second and third with red basal band with black spots and pale red marginal band, hyaline band between, with white on elements. Anal fin pale red, darker along margin; caudal fin pale red; pectoral fins red, bases dark grey with two oval, bluish marks, one above the other; pelvic fins pink.

Females with translucent greenish body, irregularly spotted with white, with large interconnecting red blotches, red and black spots on scale margins, forming a reticulated pattern; head greenish with numerous dark red spots and short bands, the darkest a diagonal band on the side of the snout.

Colour in alcohol. Males with head below eyes to pectoral fin base dark to black, body with scattered clusters of melanophores. First dorsal fin with micro-melanophores on membrane between first two spines, larger black spots on subsequent membranes, second with black spots on membranes basally and third and anal fin with dusky bands along margins.

Females with reticulated pattern of dark half-bars characteristic of the females of many species of the genus.

DISTRIBUTION (Fig. 1). *Helcogramma steinitzi* is known from the Red Sea, the coasts of Yemen and Oman and the Persian Gulf.

COMPARISONS. The only other species of *Helcogramma* that occurs sympatrically with *H. steinitzi*, *H. obtusirostre* has a smaller head (3.3–3.7 in SL vs 3.0–3.5 for *H. steinitzi*), a blunter snout, 18–19 anal-fin rays (usually 20 for *H. steinitzi*) and a lower first dorsal fin in males (about equal in height to the second for *H. steinitzi*). In life the males of the two species can be easily distinguished. Mature *H. obtusirostre* males are much darker than *H. steinitzi* males, often nearly black, with two distinctive pale, narrow saddles and a blue line from the corner of the mouth to the hind margin of the pre-opercle. *H. steinitzi* is compared to the other two species of the *H. steinitzi* species group under *H. microstigma*.

Material examined. **Red Sea**: HUJ 17628 (37.2 & 38.6 mm), Ras Burka, and HUJ 18280 (33.8 mm), Elat; USNM 205824 (7: 21.1–38.0 mm), USNM 205833 (17: 16.4–35.6 mm) and USNM 205791 (8: 20.5–25.2 mm), all paratypes from Aqaba.

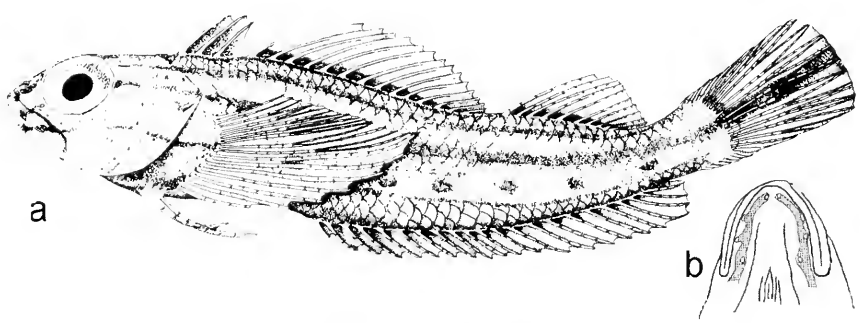


Fig. 16. *Helcogramma striata*. **a**, paratype, USNM 221916, male, 24.5 mm SL, Miyake-jima, Japan (from Hansen 1986.); **b**, mandibular pores.

Helcogramma striata Hansen

Figs. 1 & 16; Plate 2

Helcogramma striata Hansen 1986: 349, fig. 18 (Miyake Jima, Japan, in part); Fricke 1994: 437.
Helcogramma striatum Fricke 1997: 480.

Diagnosis. Dorsal fins III + XIII–XIV + 10–12 (usually III + XIII + 11); anal fin I, 19–20 (usually 20 rays); pectoral fins 16: usually 2, 7, 7. Lateral line 17–18 (mostly 17) tubed scales, ending below the posterior end of the second dorsal fin; total lateral scales 38 or 39; transverse scales 11/10. Vertebrae 10 + 25–27; 1 free pterygiophore between second and third dorsal fins. (See table 7 for geographic variation). Mandibular pores 3 + 2 + 3 (Fig.16b). Head length 3.3–3.6 (3.5) in SL; eye 2.3–2.6 (2.5), maxilla 2.0–2.3 (2.2) in head length.

Nape scaled, belly naked, scales running to bases of dorsal and anal fins; 2–3 rows of small scales at base of caudal fin. Lateral line continues straight from lateral extrascapular without curve. First dorsal fin about half height of second. Eyes large, snout short, half length of maxilla; mouth down-turned and large, maxilla reaching vertical through mid-pupil. Both jaws with band of conical, slightly recurved teeth and larger, similar teeth, evenly spaced along outer and inner margins; vomer with curved band of relatively large teeth; palatines with long toothplates with large teeth. Orbital cirrus absent.

Live colour (from Hansen, 1986 and a colour photograph by David Grey). Body of males red dorsally, green to dark blue ventrally, with longitudinal bluish stripes on each side, running from snout to caudal peduncle: dorsal-most from top of head along the first and second scale rows to the top of the caudal peduncle; middle stripe from hind margin of eye onto caudal peduncle and along centre of caudal fin; ventral-most along level of bottom of eye, across opercle and pectoral-fin base, and along margin of dark ventrum. Midway between lower two stripes is a series of 6 or 7 green-blue spots. Belly whitish. Head above ventral-most stripe red with blue-white marks, lips red with stripes continuing onto them; throat white. First dorsal fin red with grey-blue spots on membranes; second and third dorsal fins with red elements and a blue-green band basally; caudal fin with red or rays and central blue stripe; anal fin uniformly dark blue; pectoral fins with pink rays; pelvic-fin rays red, membrane pink.

Females are identical in colour, but paler.

Colour in alcohol. While Hansen noted that there was no sexual dichromatism, there is some evidence in preserved specimens.

Males with three longitudinal series of brownish-black spots, the first extending from upper, posterior quadrant of eye to end of third dorsal fin, second from posterior margin of eye, along post-orbital sensory canal to upper caudal-fin base, and third series, a broad stripe extending from beneath lower half of pectoral fin to lower caudal peduncle and to base of anal fin. Between this stripe and below the one above it is a broad, immaculate stripe along the midside with 6–8 clusters of centrally-placed, evenly-spaced brown spots, from beneath pectoral fin to below third dorsal fin. Centre of belly immaculate. First dorsal fin with many small melanophores; second dorsal fin with basal band of brown spots and tiny spots on the fin membranes; third dorsal fin with narrower basal band and tiny spots on the fin membranes. Caudal fin with series of brown spots running along the centre; anal fin liberally covered with black and brown spots, except the tips of the rays, which are immaculate. Pectoral-fin base spotted, with brown spots along proximal portion of rays and tiny spots on membranes. Head with narrow stripe of spots from upper lip, below eye to edge of preopercle, and with patch of brown spots on the upper lip and snout and line of spots along margin of preopercle.

Females lack the broad, lower body band, having a narrow band of spots below the clear band. Large females may be finely spotted between this band and anal-fin base. The mid-body clusters also are smaller and may be absent in small/immature specimens.

Comparisons. In the Western Indian Ocean (*sensu lato*) *H. striata* occurs only in Sri Lanka, where it can be distinguished from all other *Helcogramma* species by its striped body.

Remarks. Although I have examined only about 20 specimens from two localities I have not found as wide a range of counts as recorded for this species by Fricke (1997: 488 & 489; see Table 7). However, the counts I have made separate the Western Indian Ocean and

Table 7. Counts for *H. striata* from different localities.

Locality	D2 spines			D3 rays			Anal fin rays				Caudal vertebrae			Lateral line scales					
	13	14	15	10	11	12	19	20	21	22	25	26	27	16	17	18	19	20	21
Sri Lanka n = 8	6	1		1	7		2	5			4	4			5	2			
Phuket, Thailand n = 38	35	3		8	29	1	*31	5			1	23	5	4	15	5	5		
Penghu Islands n = 11		10	1	2	9			2	8	1	1	4	5			1	4		4

* One with 17 rays

Taiwanese material quite clearly, with a shift of 13 to 14 second dorsal-fin spines, 20 to 21 anal-fin rays and mean of 17 to a mean of 19 tubed lateral-line scales. While such differences are more than have been used to distinguish between other species in the genus (*Helcogramma obtusirostre* and *H. rharhabe*, for example), these seem to be locality dependent (environmentally determined?). For the present I accept these as a single species and not two species, one in the Indian Ocean and one in the Western Pacific, particularly as there appears no disparity in colour pattern between the populations. A more detailed investigation may prove otherwise.

Helcogramma striata is probably the sister species of *H. maldivensis*, from which it is distinguished by colour pattern and dorsal-fin ray counts: *H. striata* has a mode of 11 rays, *H. maldivensis* a mode of 10. It is interesting to note that while there is little sexual dichromatism in *H. striata*, possibly unique within the genus, *H. maldivensis* does show sexual dichromatism, with the males darker and more brightly coloured than the females.

DISTRIBUTION (Fig. 1).
Sri Lanka and eastwards, to Thailand, northern Australia, throughout Indonesia, to Japan and the Western Pacific Ocean to Kiribati.

Material examined. **Sri Lanka**: SAIAB 30430 (6: 19.7–23.7 mm) and SAIAB 30435 (17.2 & 20.3 mm), Trincomalee. **Thailand**: ROM 78140 (12: 17.5–22.9 mm); ROM 78142 (12: 8.8–21.5 mm); ROM 78143 (12: 16.0–22.4 mm); ROM 78146 (12: 18.0–24.7 mm), Phuket. **Taiwan**: SAIAB 35675 (11: 24.1–30.7 mm), Penghu Islands.

DISCUSSION

It is obviously not ideal to review the species of the Western Indian Ocean without including material from Indonesia and the Western Pacific Ocean, particularly when it is known that species closely related to ones in the Western Indian Ocean exist in the Western Pacific.

In their investigation into the historical biogeography of Indo-western Pacific coral reef fauna Santini & Winterbottom (2002) divided the region into a number of areas on the basis of the endemism exhibited by the taxa used in their study. They noted (2002:197)–as have Knowlton (1993) and Gill & Kemp (2002)–that little is known about the dispersal of the planktonic eggs and larvae of marine organisms, although this is changing rapidly, requiring a major rethink about larval fish dispersal–see Fisher et al. 2005 and references therein. Knowlton and Gill & Kemp (*op. cit.*) have challenged the concept of widespread Indo-Pacific shore fishes, stating that widespread species are a reflection of "current taxonomic practice and understanding" (*ibid.* p.165), and argue that many currently accepted widespread species are probably complexes of closely related species.

With but three exceptions–*Helcogramma larvata*, *H. striata* and *H. fuscopinna*– the dorsal and anal fin counts of the other 12 Western Indian Ocean species are almost identical, with 13–14 spines in the second dorsal fin, 9–11 rays (6 with 10 rays) in the third dorsal fin, and 18–20 (usually 19–20) rays in the anal fin (an exception of *H. maldivensis* with 22 rays). There is a concomittant similarity in vertebral counts and total lateral scale counts.

These findings do not substantiate Fricke's recording of variations of 4 and 5 (and sometimes as many as 7) dorsal-fin spine or ray, or anal-fin ray counts. For example he (1994: 416ff, 1997: 428ff) examined more than 200 specimens of *Helcogramma chica* from localities ranging from Thailand to Moorea and records ranges in counts of 12–16 second-dorsal fin spines (mode 14), 8–12 third-dorsal fin rays (mode 10) and 17–21 anal-fin rays (mode 19). These are greater variations than I (Holleman 2006) or Williams & McCormick (1990) or Williams & Howe (2003) have recorded for *any* tripterygiid species. Fricke's counts are clearly inaccurate.

ACKNOWLEDGEMENTS

Barry Hutchins kindly checked *H. chica* specimens from Christmas and Cocos-Keeling Islands. Robin Stobbs provided the derivation of the name *alkamr* and its history. Specimens were kindly loaned by the Bishop Museum, Honolulu, the Hebrew University of Jerusalem, the Royal Ontario Museum and the National Museum of Natural History, Smithsonian Institution. David Catania, California Academy of Sciences, checked the types of *H. ellioti*. Special thanks to Arnold Suzamoto, Bishop Museum, Honolulu, who checked various specimens for me, including the types of *H. maldivensis* and *H. larvata*, made counts, provided one of the latter on loan to be illustrated, and arranged for radiographs to be made of the types in the Bishop Museum. Special thanks to Jack Randall and Rick Winterbottom for the use of his photographs of several of the species. Without the access Jack so generously gives to his photographs, many a paper on Indo-Pacific fishes would be much less 'complete'. David Grey provided the underwater photograph of *H. striata*, and Sergei and Rick Winterbottom. Bogordski those of *H. obtusirostre*. Willem Coetzer of SAIAB compiled the distribution map, and Elaine Heemstra made most of the excellent drawings. Support and research facilities are generously provided by the South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown.

LITERATURE CITED

CLARK, E. 1979. Red Sea fishes of the family Tripterygiidae with descriptions of eight new species. *Israel Journal of Zoology*, **28**: 65–113.

FISHER, R., J. M. LEIS, D. L. CLARK & S. K. WILSON. 2005. Critical swimming speeds of late-stage coral reef fish larvae: variation within species, among species and between locations. *Marine Biology* **147**: 1201–1212.

FRICKE, R. 1994. *Tripterygiid Fishes of Australia, New Zealand and the Southwest Pacific Ocean (Teleostei)*. Koeltz Scientific Books, Königstein. ix, 585 pp.

FRICKE, R. 1997. *Tripterygiid Fishes of the Western and Central Pacific (Teleostei)*. Koeltz Scientific Books, Königstein. ix, 607 pp.

FRICKE, R. & J. E. RANDALL. 1992. Tripterygiid fishes of the Maldive Islands, with descriptions of two new species (Teleostei: Blennioidei). *Stuttgarter Beiträge zur Naturkunde Serie A (Biologie)* No. 484, 1–13.

GILL, A.C. & J. M. KEMP. 2002. Widespread Indo-Pacific shore fish species: a challenge for taxonomists, biogeographers, ecologists and fishery and conservation managers. *Environmental Biology of Fishes* **65**: 165–174.

HANSEN, P. E. HADLEY. 1986. Revision of the tripterygiid fish genus *Helcogramma*, including descriptions of four new species. *Bulletin of Marine Science* **38**(2): 313–354.

HERRE, A. C. W. T. 1944. New fishes from Johore and India. *Proceedings of the Biological Society of Washington* **57**:45–52.

HOLLEMAN, W. 1982. Three new species and a new genus of tripterygiid fishes (Blennioidei) from the Indo-West Pacific Ocean. *Annals of the Cape Provincial Museums* (Natural History) **14**(4): 109–137.

HOLLEMAN, W, 2006. Fishes of the *Helcogramma steinitzi* species group (Blennioidei: Tripterygiidae) from the Indian Ocean, with descriptions of two new species. aqua, *Journal of Ichthyology and Aquatic Biology* **11**(3): 89–104.

HUBBS, C.L. & K.F. LAGLER. 1958. Fishes of the Great Lakes Region. *Cranford Institute Scientific Bulletin* **26**: 1–213.

KLUNZINGER, C. B. 1871. Synopsis de fisches des Rothen Meeres. *Verhandlungenen der kaiserlich-königlichen zoolochish- botanischen Gesellenschaft in Wien* **21**: 441–668.

KNOWLTON, N. 1993. Sibling species in the sea. *Annual Review of Ecology and Systematics* **24**: 189–216.

LAL MOHAN, R. S. 1968. On a Collection of Blennies from Gujarat Coast with Some New Records. *Journal of the Marine Biological Association of India* **10**(1): 118–125.

LAL MOHAN, R. S. 1971. *Helcogramma shinglensis*, a new species of tripterygiid fish from Gulf of Mannar with a key to the fishes of the family Tripterygiidae of the eastern and central Indian Ocean. *Senckenbergiana Biologica* **52**(3/5): 219–223.

LUBBOCK, R. 1980. The shore fishes of Ascension Island. *Journal of Fish Biology* **17**: 283–303.

MARSHALL, N. B. 1952. The Manihine Expedition to the Gulf of Aqaba, 1948–49. *Bulletin of the Museum (Natural History), Zoology* **1**(8): 221–252.

MCCULLOCH, A.R. & E.R. WAITE. 1918. Some new and little known fishes from South Australia. *Records of the South Australian Museum* **1**(1): 39–78.

OWEN, D. R. 1994. *Ubukhosi neenkokeli*. Albany Museum, Grahamstown. 94 pp.

RANDALL, J. E. 1995. *Coastal Fishes of Oman*. University of Hawai'i Press, Honolulu. 439 pp.

RANDALL, J. E. & E. CLARK. 1993. *Helcogramma vulcana*, a new triplefin fish (Blennioidei: Tripterygiidae) from the Banda Sea, Indonesia. *Revue francaise d' Aquariologie* **20**(1): 27–32.

ROSENBLAFF, R. 1960. (Descriptions of new species of *Helcogramma*). In: Schultz, L.P. Fishes of the Marshall and Marianas Islands, Vol. 2. *United States National Museum Bulletin* 202: 1–438.

SANTINI, F. & R. WINTERBOTTOM. 2002. Historical biogeography of Indo-western Pacific coral reef biota: is the Indonesian region a centre of origin? *Journal of Biogeography* **29**: 189–205.

SARUWATARI, T., J. A. LOPEZ & T. W. PIETSCH. 1997. Cyanine Blue: a versatile and harmless stain for specimen observation. *Copeia* 1997(4): 840–841.

SHAMSUL HODA, S. M. 1983. First record of *Helcogramma ellioti* (Family : Tripterygiidae) from Pakistan. *Biologia* **29**(1): 41–46.

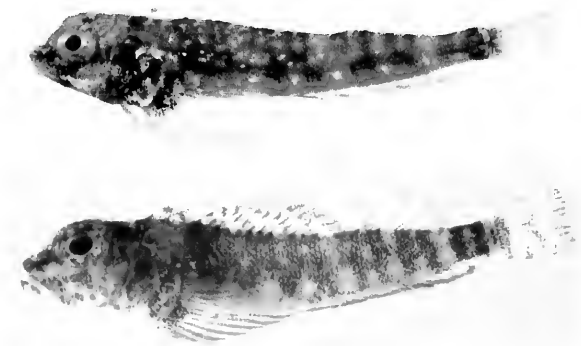
SPRINGER, V. G. 1968. Osteology and classification of the fishes of the family Blenniidae. *Bulletin of the United States National Museum* **248**: 1–80.

TALWAR, P. K. & T. K. SEN. 1971. On some fishes the Madras coast with description of a new species of the family Clinidae. *Records of the Zoological Survey of India* **65**(1–4): 243–251.

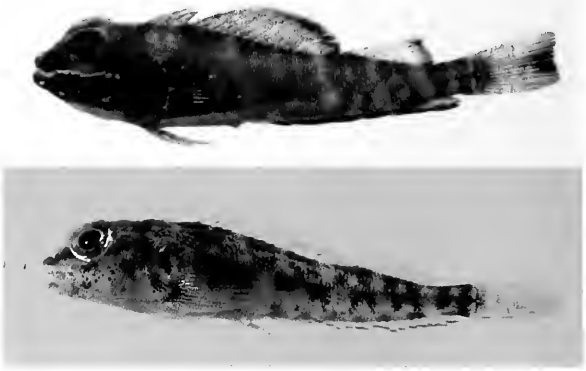
WILLIAMS, J. T. & J. C. HOWE. 2003. Seven new species of the triplefin genus *Helcogramma* (Tripterygiidae) from the Indo-Pacific. *aqua, Journal of Ichthyology and Aquatic Biology* **7**(4):151–176.

WILLIAMS, J. T. & C. J. MCCORMICK. 1990. Two new species of the triplefin fish genus *Helcogramma* (Tripterygiidae) from the Western Pacific Ocean. *Copeia* **1990**(4): 1020–1030.

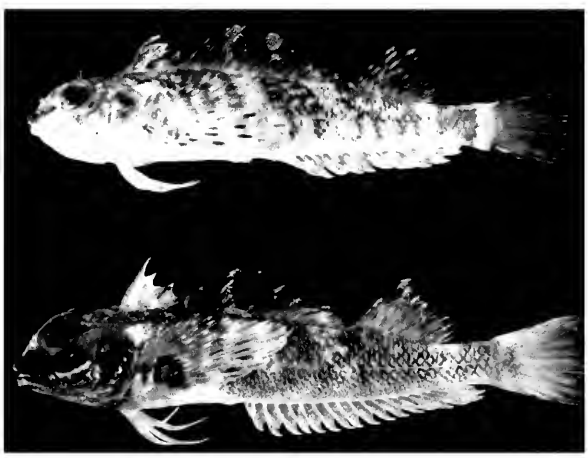
PLATE 1



Helcogramma alkamr, ROM 73734, male (above), 27.5 mm SL, holotype, Mayotte, Comoro Islands (R. Winterbottom); female (below), 16 mm SL, Mahé, Seychelles (P. C. Heemstra).



Helcogramma fuscopinna, male (above), Anjouan, Comoro Islands (R. Winterbottom); female (below), 30.0 mm SL, Rodrigues (P. C. Heemstra).

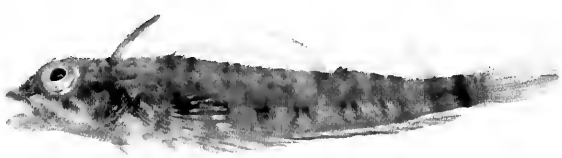


Helcogramma ellioti, BPBM 27684, female (above), 30 mm SL; male (below), 33 mm SL, Kovalam, India (J. E. Randall).

Helcogramma maldivensis, paratype, BPBM 32976, male, 27.6 mm SL, North Male Atoll, Maldive Islands (J. E. Randall).

Helcogramma maldivensis, ~ 30 mm TL, Maldive Islands (J. E. Randall).

Helcogramma ememes, BPBM 29290, male (above), 23 mm SL; female (below), 24 mm SL, Aride, Seychelles (J. E. Randall).



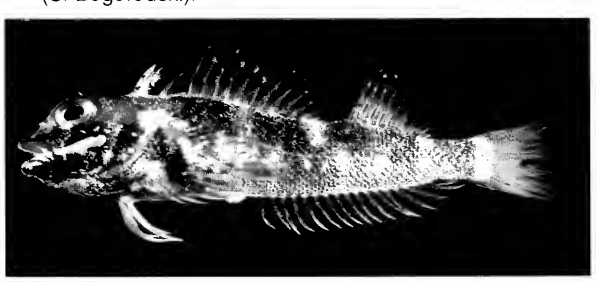
Helcogramma microstigma, ROM 73410, male, 31.3 mm SL, Comore Islands (R. Winterbottom).

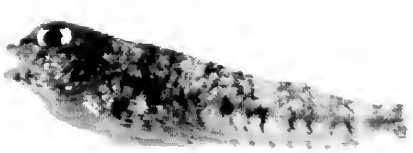
PLATE 2

Helcogramma obtusirostre, male (above), 30.0 mm SL; female (below), 28.0 mm SL, Oman (J. E. Randall)

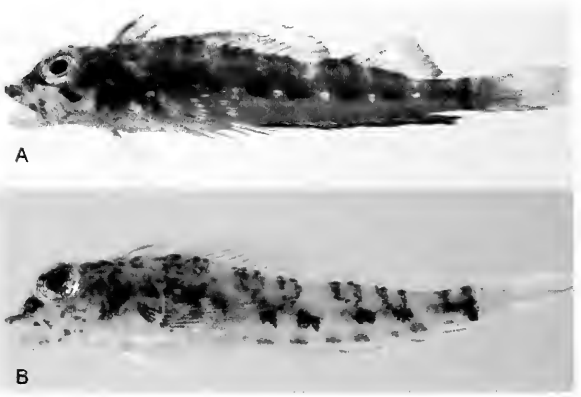
Helcogramma obtusirostre, male, Sharm el Sheik, Egypt (S. Bogordski).

Helcogramma obtusirostre, female, Sharm el Sheik, Egypt (S. Bogorodski).

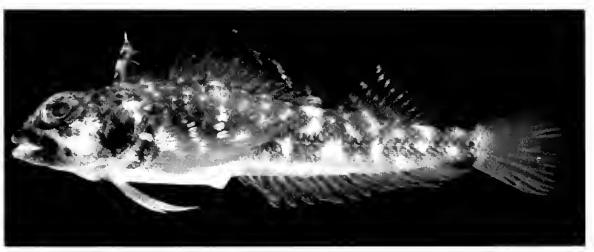




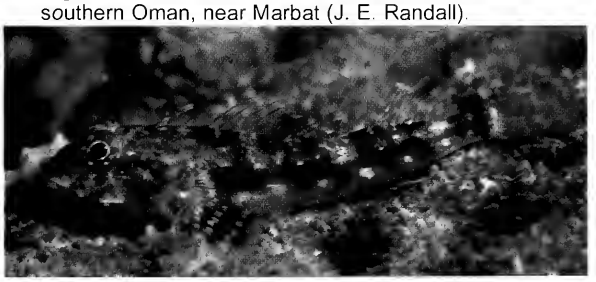
Helcogramma rharhabe, male (above), 34 mm SL, (J. E. Randall); female (below), 31.0 mm SL, Sodwana Bay,



Helcogramma rosea, holotype, ROM 76679, male, 34.4 mm SL (above), and, paratype, ROM 76680, female, 27.6 mm SL (below),Phuket, Thailand (R. Winterbottom).



Helcogramma steinitzi, BPBM 35926, male, 33 mm SL, southern Oman, near Marbat (J. E. Randall).



Helcogramma steinitzi, female, ~45 mm TL, Masirah Island, Oman (J. E. Randall)

Helcogramma striata, WIO, locality unknown (D. Grey)

Helcogramma striata, Ogasarawa Islands, Japan (Yukihiko Otsuka)

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